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1967–1968

CAMBRIDGE, MASS. U.S.A.

1969

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CONTENTS

BREVIORA

MUSEUM OF COMPARATIVE ZOOLOGY

NUMBERS 265–295

1967

No. 265. New land-locked fish species of the genus *Galaxias* from North Auckland, New Zealand. By R. M. McDowall. 11 pp. April 6.

No. 266. A new species of *Vesicomya* from the Caribbean Sea (Mollusca: Bivalvia: Vesicomyidae). By Kenneth Jay Boss. 6 pp. April 6.

No. 267. A new generic arrangement for some Australian scincid lizards. By Allen E. Greer. 19 pp. June 29.

No. 268 The ecology and behavior of two sympatric *Lygodactylus* geckos. By Allen E. Greer. 19 pp. June 29.

No. 269. Two new species of *Amphitarsus* (Ophiuroidea) from the Western North Atlantic. By Amy Schoener. 9 pp. June 29.

No. 270. Additions to the unionid fauna of the Gulf drainage of Alabama, Georgia, and Florida (Mollusca: Bivalvia). By Richard I. Johnson. 21 pp. June 29.

No. 271. *Chelonia depressa* Garman re-investigated. By Ernest E. Williams, Alice G. C. Grandison, and Archie F. Carr, Jr. 15 pp. November 17.

No. 272. The ecological distribution of the anoline lizards around Kingston, Jamaica. By A. Stanley Rand. 18 pp. November 17.

No. 273. Studies on neotropical Pompilidae (Hymenoptera). III. Additional notes on *Epipompilus* Kohl. By Howard E. Evans. 15 pp. November 17.

No. 274. The genus *Nops* (Araneae, Caponiidae) in Panama and the West Indies. By Arthur M. Chickering. 19 pp. November 17.

No. 275. A new scincid lizard from the northern Solomon Islands. By Allen E. Greer and Fred Parker. 20 pp. November 17.

No. 276. The generic relationships of the African scincid genus *Eumecia*. By Allen E. Greer. 9 pp. November 24.

No. 277. *Lestidium bigelowi*, a new species of paralepidid fish with photophores. By Michael J. F. Graae. 10 pp. November 24.

No. 278. Notes on the emberizine sparrow *Rhynchospiza stolzmanni*. By Raymond A. Paynter, Jr. 6 pp. November 24.

No. 279. A second skink with fragmented head scales from Bougainville, Solomon Islands. By Allen E. Greer and Fred Parker. 12 pp. November 24.

1968

No. 280. The *notatus* group of *Sphaerodactylus* (Sauria, Gekkonidae) in Hispaniola. By Benjamin Shreve. 28 pp. March 19.

No. 281. Additional notes on batoid fishes from the Western Atlantic. By Henry B. Bigelow and William C. Schroeder. 23 pp. April 5.

No. 282. The extinct baboon, *Parapapio jonesi*, in the early Pleistocene of northwestern Kenya. By Bryan Patterson. 4 pp. April 5.

No. 283. Scythian ammonoids from Timor. By Bernhard Kummel. 21 pp. April 5.

No. 284. The relationships of *Anolis* of the *roquet* species group (Sauria: Iguanidae) — III. Comparative study of display behavior. By George C. Gorman. 31 pp. April 5.

No. 285. The genera of puffbirds (Bucconidae). By G. W. Cottrell. 5 pp. April 5.

No. 286. The status of *Nesogalaxias neocaledonicus* (Weber and de Beaufort) (Pisces, Galaxiidae). By R. M. McDowall. 8 pp. April 5.

No. 287. The sequence of genera in the Estrildidae (Aves). By Ernst Mayr. 14 pp. April 5.

No. 288. The epidermal glands of *Lygodactylus* (Gekkonidae, Lacertilia). By P. F. A. Maderson. 35 pp. May 29.

No. 289. The genus *Miagrammopes* (Araneae, Uloboridae) in Panama and the West Indies. By Arthur M. Chickering. 28 pp. May 29.

No. 290. Geographic Variation in the Hispaniolan frog *Eleutherodactylus wetmorei* Cochran. By Albert Schwartz. 13 pp. May 29.

No. 291. A new species of *Tribolonotus* (Lacertilia: Scincidae) from Bougainville and Buka, Solomon Islands, with comments on the biology of the genus. By Allen E. Greer and Fred Parker. 23 pp. May 29.

No. 292. Herpetogeography of Puerto Rico. V. Description of a new species of *Sphaerodactylus* from Desecheo Island. By Harold Heatwole. 6 pp. May 29.

No. 293. Intra- and interspecific chromosome variation in the lizard *Anolis cristatellus* and its closest relatives. By George C. Gorman, Richard Thomas, and Leonard Atkins. 13 pp. May 29.

No. 294. Distribution and biology of the opisthoproctid fish *Winteria telescopa* Brauer 1901. By Richard L. Haedrich and James E. Craddock. 11 pp. May 29.

No. 295. The Chañares (Argentina) Triassic reptile fauna. IV. The dicynodont fauna. By C. Barry Cox. 27 pp. May 29.

INDEX OF AUTHORS

BREVIORA

MUSEUM OF COMPARATIVE ZOOLOGY

NUMBERS 265–295

1967–1968

	No.
ATKINS, LEONARD	293
BIGELOW, HENRY B.	281
BOSS, KENNETH JAY	266
CARR, ARCHIE F., JR.	271
CHICKERING, ARTHUR M.	274, 289
COTTRELL, G. W.	285
COX, C. BARRY	295
CRADDOCK, JAMES E.	294
EVANS, HOWARD E.	273
GORMAN, GEORGE C.	284, 293
GRAAE, MICHAEL J. F.	277
GRANDISON, ALICE G. C.	271
GREER, ALLEN E.	267, 268, 275, 276, 279, 291
HAEDRICH, RICHARD L.	294
HEATWOLE, HAROLD	292
JOHNSON, RICHARD I.	270

No.

Kummel, Bernhard 283

Maderson, P. F. A. 288

Mayr, Ernst 287

McDowell, R. M. 265, 286

Parker, Fred 275, 279, 291

Patterson, Bryan 282

Paynter, Raymond A., Jr. 278

Rand, A. Stanley 272

Schoener, Amy 269

Schroeder, William C. 281

Schwartz, Albert 290

Shreve, Benjamin 280

Thomas, Richard 293

Williams, Ernest E. 271

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. 6 APRIL, 1967 NUMBER 265

NEW LAND-LOCKED FISH SPECIES OF THE GENUS *GALAXIAS* FROM NORTH AUCKLAND, NEW ZEALAND[1]

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Museum of Comparative Zoology, Harvard University

ABSTRACT: Two species of *Galaxias* Cuvier (Galaxiidae) are described from small land-locked coastal dune lakes in North Auckland, New Zealand. They are small shoaling species similar to and apparently derived from the sea-going *Galaxias maculatus attenuatus* (Jenyns).

INTRODUCTION

In the New Zealand Galaxiidae, speciation appears to be taking place by the land-locking of sea-going species. This is a pattern familiar in the Northern Hemisphere Salmonidae, and also in the Southern Hemisphere in the Retropinnidae (McDowall, 1965). Stokell (1964) described a new species of *Galaxias* (*G. parrishi*), which he considered to be a land-locked derivative of *G. maculatus ignotus,* and noted another land-locked form from Victoria, Australia. The writer (McDowall, 1966) noted a similar form collected from another Victorian lake (see Pollard, 1964), and the occurrence of further such derivatives from *G. maculatus attenuatus,* in New Zealand coastal lakes.

About 15 years ago, the New Zealand Marine Department conducted a survey of the chain of small lakes on the west coast of the North Island of New Zealand, to determine their ecology in relation to the introduction of suitable game fishes. In their report on this survey, Cunningham et al. (1953) described the fish faunas of these lakes as follows: "Various species of *Galaxias, Gobiomorphus,* and *Retropinna* were recorded," and they listed in a table the lakes from which these genera were taken. In 1963, the writer examined a sample of *G. maculatus attenuatus*-like fishes from one of these lakes, which, on close examination, appeared to

[1] Fisheries Research Publication No. 93.

be distinct from *G. maculatus attenuatus* in a number of details. Because this sample was rather old, it was felt desirable to recollect the fish, before description, and this was done in March 1965. Large samples of *Galaxias* were collected from Lake Waiparera, a few miles north of Kaitaia, and from Upper Lake Rototuna, on the peninsula west of the northern arm of Kaipara Harbor (Fig. 1). Inasmuch as these lakes are land-locked, it was to be expected that the *Galaxias* populations would differ morphologically and behaviorally from *Galaxias maculatus attenuatus.*

Figure 1. Locality map of North Island, New Zealand, showing location of: 1. Lake Waiparera, 2. Lake Rototuna.

Being land-locked, their life cycles are also necessarily modified from that of *G. maculatus attenuatus* which has marine juveniles.

Examination of the fresh samples from these two lakes, showed them to be distinct from *G. maculatus attenuatus* and from each other. They do not resemble any other New Zealand species of *Galaxias.* Characters suggesting relationship to *G. maculatus attenuatus,* apart from their general appearance and coloration, include shoaling behavior as adults, forked caudal fins, similar dentition, lack of pyloric caeca, and the long, many-rayed anal fin.

The isolation of sea-going species in small lakes, as appears to have taken place in these instances, poses a problem in species delimitation. The alternatives lie between describing each isolate as a distinct species or subspecies, or including all the populations in a single, widely variable species, derived from the parent sea-going species. Since there has been a fundamental change in the life history pattern of the land-locked species, it seems likely that the parent and derivative species have acquired reproductive isolating mechanisms. This conclusion is supported by the fact that the derivative populations have developed characteristic morphological differences from the parent population. The specific distinctness of the two derivative populations under examination is another problem. Ideally, breeding experiments and behavioral studies of the two populations would be desirable to provide the answers, but these are outside the scope of the present study. On examining the morphological differences between the two populations, it seemed likely that they were independently derived from the parent stock and therefore more closely related to the parent than to each other. The population in Lake Rototuna is, from both morphological and geological considerations, probably an earlier derivative of *G. maculatus attenuatus* than is the Lake Waiparera population. Lake Rototuna occurs in well stabilized rolling sand dunes, once covered in bush, at an altitude of 300 ft. (91 m), whilst Lake Waiparera is in still shifting sand dunes, about a hundred feet (36 m) above sea level. Corresponding to their apparent difference in age, and perhaps to differing ecological conditions in the two lakes, the degree to which these species have diverged from their common parent species differs greatly. The differences are most obvious in vertebral count, a character which has proved useful in separating *Galaxias* species in New Zealand. Assuming relationship to *G. maculatus attenuatus,* the Lake Rototuna population has traversed the full range of vertebral number in the New Zealand Galaxiidae, from the maximum in *G. maculatus attenuatus* of 59-64, to a minimum of 47-50. The vertebral number in the Lake Waiparera population is also reduced and almost completely disjunct from both *G. maculatus attenuatus* and the Lake Rototuna population, viz. 54-59 (Fig. 2).

The direction of divergence from *G. maculatus attenuatus,* seen in the two derivatives, varies; sometimes the counted structures are fewer in number, as in vertebrae and most of the fin-ray counts (Fig. 3). In the case of gill rakers (Fig. 2), in contrast, *G. maculatus attenuatus* has a total count on the first arch of 13-17, the Waiparera fish 15-17, and the Rototuna fish 18-23. These data

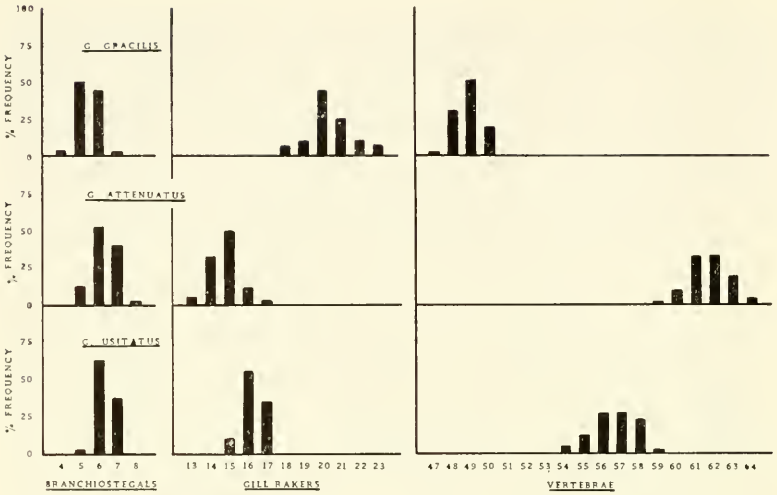

Figure 2. Frequency distribution for counts of branchiostegals, gill rakers, and vertebrae in *Galaxias gracilis, G. maculatus attenuatus,* and *G. usitatus.*

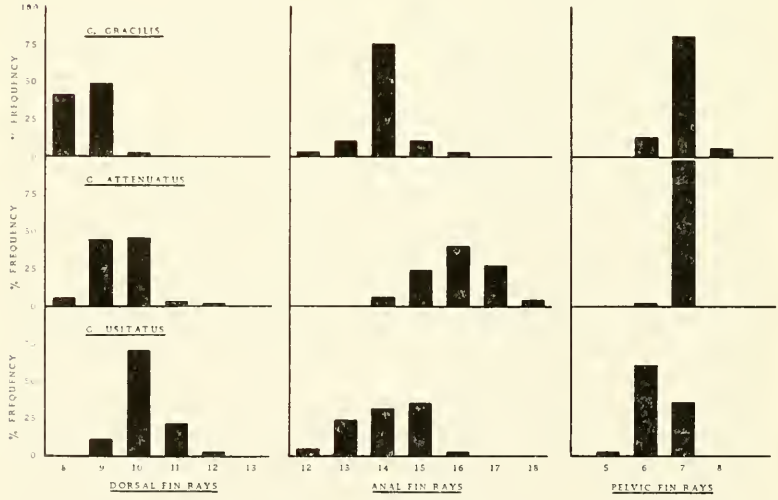

Figure 3. Frequency distribution for counts of dorsal, anal, and pelvic fin rays in *Galaxias gracilis, G. maculatus attenuatus,* and *G. usitatus.*

suggest that the meristic distinctions may not be simply a case of temperature related differences. Differences were also found to occur in body proportions. In some cases both the derivatives diverged from *G. maculatus attenuatus* in the same direction (Fig. 4-2, 4-5), the measured structure being proportionately either

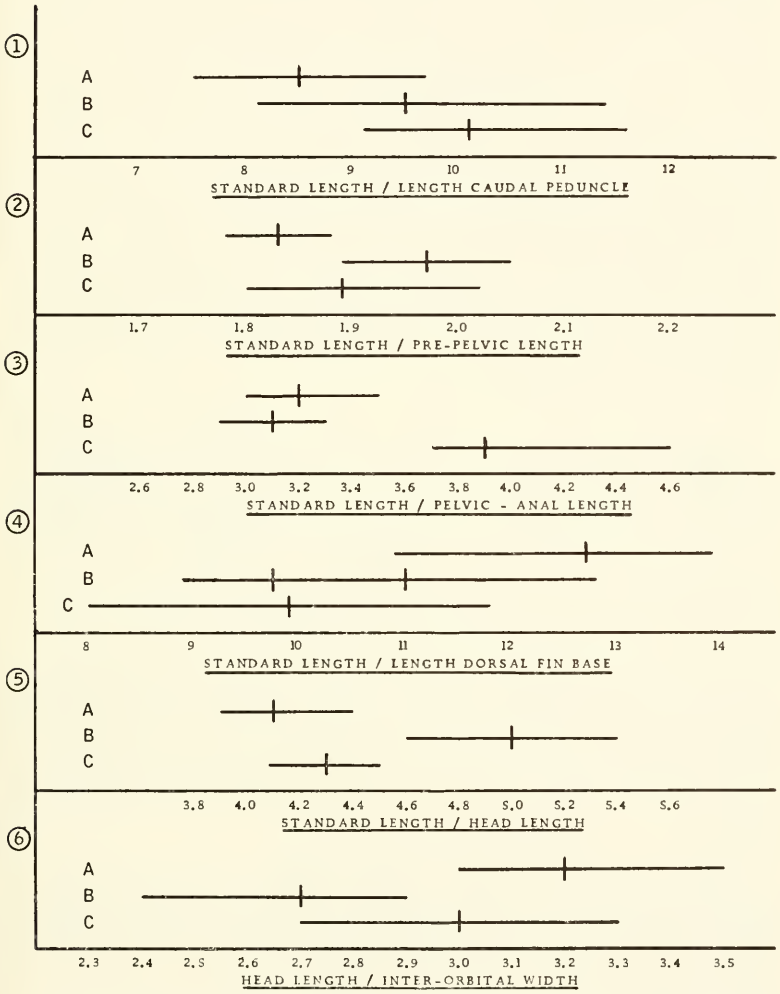

Figure 4. Ranges for proportional measurements in *Galaxias gracilis* (A), *G. maculatus attenuatus* (B), and *G. usitatus* (C).

larger or smaller in both derivatives than in *G. maculatus attenuatus*. In other cases, the divergence has gone in opposite directions, and the range for *G. maculatus attenuatus* was found to lie between the ranges for the derivative populations (Figs. 4-1, 4-4).

These data indicate that each of the two populations should be regarded as a full species, distinct from *G. maculatus attenuatus* and from each other.

SYSTEMATIC DESCRIPTION

Galaxias gracilis[1] n.sp.

Figure 5; Table 1a.

Holotype: Deposited in collection of Fisheries Research Division, New Zealand Marine Department.

Paratypes: Dominion Museum, New Zealand. Reg. No. 4499; Museum of Comparative Zoology, Harvard University, No. 45053; Smithsonian Institution Fish Collection No. USNM 201224.

Type locality: Upper Lake Rototuna, Kaipara Harbour, North Auckland, New Zealand.

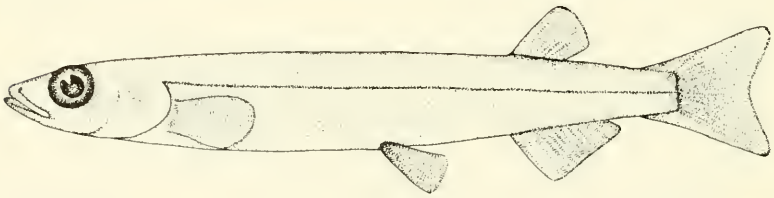

Figure 5. *Galaxias gracilis* n.sp. Length to caudal fork, 59 mm.

Description: A small, slender, shoaling species with long head, low vertebral count and rearward placement of the pelvic fins. Maximum known fork length 62.5 mm. D i-iii, 7-10; C 16; A i-iii, 12-16; Pel 6-8; Pec 12-14; Branchiostegals 4-6; Vertebrae 47-50; Gill-rakers 5-7 (upper), 13-17 (lower limb of first arch), total 18-23.

Trunk cylindrical, slender, somewhat depressed on head, laterally compressed on caudal peduncle, deeper than broad. Caudal peduncle slender and short. Head small, slender, a little broader than deep, lower jaw protruding a little, or equal in length to upper; lips thin, cleft of mouth slightly oblique, extending to a

[1] Named on account of its slender form, from the Latin *gracilis*, slender.

line through anterior eye margin. Eye large, at upper head profile, with inter-orbital flat.

Mandibular and premaxillary teeth without canines, lingual teeth strong, entopterygoidal teeth moderately developed; gill-rakers strongly developed; pyloric caeca lacking.

Fins membranous and short, except anal which is long based. Distal margin of dorsal fin rounded to straight, anterior rays longest. Anal origin more or less below dorsal origin, distal margin of fin straight, anterior rays longest, maximum fin length little longer than base length. Pelvic fins inserted relatively far back, pelvic-anal interval short, fin relatively short in pelvic-anal length. Pectoral fin disposed laterally, fin short. Caudal fin forked, fin tips rounded, depth about equal to body depth.

Coloration: Trunk covered with a dense peppering of large melanophores, which intensify on the head and dorsum of the trunk, failing lateroventrally, and ventrally. Fresh material is silver in these latter areas.

Meristic variation: Dorsal rays (segmented), 7(1), 8(21), 9(23), 10(5); Caudal 15(4), 16(42), 17(4); Anal 12(1), 13(5), 14(30), 15(13), 16(1); Pelvic 6(7), 7(40), 8(3); Pectoral 12(8), 13(28), 14(14); Vertebrae 47(1), 48(16), 49(24), 50(9); Branchiostegals 4(2), 5(27), 6(21); Gill-rakers (total count) 18(2), 19(3), 20(13), 21(7), 22(3), 23(2).

Differs from *G. maculatus attenuatus* (Jenyns) in having a much lower vertebral count, fewer dorsal rays, a somewhat lower branchiostegal count and more gill rakers; also in a longer pre-pelvic length, longer head, narrower inter-orbital, larger eye, short dorsal fin base, smaller maximum size reached, and the lack of a marine whitebait juvenile stage. Differs from *G. usitatus* n.sp. in having fewer vertebrae, fewer branchiostegals, a greater number of gill rakers, a longer pelvic base-anal origin length, shorter dorsal fin base, lack of serrations on the opercular membrane and the smaller maximum size attained.

Galaxias usitatus[1] n.sp.

Figure 6; Table 1b.

Holotype: Deposited in collection of Fisheries Research Division, New Zealand Marine Department.

[1] Named on account of its lack of highly distinctive characters, from the Latin *usitatus*, ordinary.

Paratypes: Dominion Museum, New Zealand Reg. No. 4500; Museum of Comparative Zoology, Harvard University, No. 45054; Smithsonian Institution Fish Collection No. USNM 201223.

Figure 6. *Galaxias usitatus* n.sp. Length to caudal fork, 72 mm.

Type locality: Lake Waiparera, North Auckland, New Zealand.

Description: A slender, lacustrine, shoaling species, similar to *Galaxias maculatus attenuatus,* with long head, a short pelvic-anal interval, with many of the fishes examined having six rather than the more usual seven pelvic fin rays. Distinctive in the presence of fine but definite serrations on the free margin of the opercular membrane. Maximum known fork length 81.5 mm. D i-iii, 9-12; C 14-18; A ii-v, 12-16; Pel 5-7; Pec 11-15; Branchiostegals 5-7; Vertebrae 54-59; Gill-rakers 4-5, 11-13, total 15-17.

Trunk cylindrical, slender, somewhat depressed on head, laterally compressed on caudal peduncle and somewhat deeper than broad. Caudal peduncle slender and short. Head long and narrow, slender, about as deep as broad; jaws equal, prominent, cleft slightly oblique reaching to about anterior eye margin, gape rather narrow. Eye large, placed close to upper head profile, inter-orbital more or less flat, broad relative to head width. Mandibular and maxillary teeth without canines, lingual teeth strong, entopterygoidal teeth well developed; pyloric caeca lacking; gill rakers well developed; free margin of operculum finely serrate.

Fins membranous and short, except anal which is long based. Dorsal fin set well back, fin with moderately short base, distal margin of fin somewhat rounded. Anal fin origin more or less below dorsal origin; anal fin long based but greatest fin length little greater than base length, distal margin of fin about straight and inclined to body axis. Pelvic fin inserted at about mid-point of standard length, pelvic-anal length short, pelvic fin moderate in pelvic-anal interval, thus short. Pectoral fin base disposed laterally, fin short. Caudal fin forked, fin tips rounded, fin depth about equal to body depth.

Coloration: Trunk a dusky gray-brown and covered with irregular dark blotches similar to *G. maculatus attenuatus*. When alive, the lateroventral and ventral abdomen is silvery, in preserved material, largely unpigmented.

Meristic variation: Dorsal rays (segmented) 9(4), 10(28), 11(8), 12(1); Caudal 14(1), 15(4), 16(34), 17(1), 18(1); Anal 12(2), 13(10), 14(13), 15(15), 16(1), Pelvic 6(30), 7(11); Pectoral 11(1), 12(5), 13(21), 14(12), 15(2); Vertebrae 54(2), 55(5), 56(10), 57(12), 58(9), 59(3); Branchiostegals 5(1), 6(25), 7(15); Gill-rakers 15(2), 16(11), 17(7).

Differs from *G. maculatus attenuatus* in having a lower vertebral count, fewer pelvic fin rays, longer head, somewhat larger eye, shorter pelvice-anal interval; differs from *G. gracilis* in details discussed under the diagnosis of that species. It differs from both *G. maculatus attenuatus* and *G. gracilis* by the presence of serrations on the opercular margin.

DISCUSSION

The two new species described above are interpreted as land-locked derivatives of one of the New Zealand sea-going species, *G. maculatus attenuatus*. In Lake Okataina, thermal lakes district, North Island, and in one of the Kaihoka Lakes, near Cape Farewell, there are two land-locked populations of the sea-going *G. fasciatus* Gray. The upland-alpine lake species *G. koaro* Phillipps and *G. lynx* Hutton are also envisaged, by the writer, as freshwater derivatives of *G. brevipinnis* Günther, a species with marine stages. It was suggested (McDowall, 1965), that *Retropinna abbreviata* McDowall and *R. lacustris* Stokell had speciated under similar circumstances — in isolation, in lakes cut off from the sea with a migratory population captured in the impounded water body. Looked at from this perspective, the distribution patterns of some of the apparently younger species in New Zealand's freshwater fish fauna make greater sense, e.g. *G. lynx,* present in alpine lakes all along the eastern side of the main divide of the South Island, to the west of the divide in the Nelson Lakes district, with, according to the arrangement of Stokell (1949) a highly disjunct population in Lake Waikaremoana, near East Cape in the North Island. This pattern appears best explained by derivation of the freshwater lacustrine form, probably several times, from the parent species *G. brevipinnis*. *G. koaro* probably has the same mode of derivation, from *G. brevipinnis,* one or several times, in the lakes of the volcanic plateau of the North Island, and further study may well suggest that *G. lynx* and *G. koaro* are conspecific.

This view of speciation in the Galaxiidae probably supplies the key to understanding much of the fauna, both phylogenetically and zoogeographically.

ACKNOWLEDGEMENT

The writer is grateful to Dr. Giles W. Mead for his advice and for reading the manuscript, and to Messrs. K. F. Maynard and W. Skrzynski for assistance in collecting the specimens. The financial support of a New Zealand National Research fellowship during the study is gratefully acknowledged.

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(Received 10 October, 1966.)

TABLE 1.

Morphometric variation in *Galaxias gracilis* and *G. usitatus*.

Ratio	a. *G. gracilis*	b. *G. usitatus*
Standard length/Body depth at vent	8.25-9.50	7.70-10.08
Standard length/Caudal peduncle length	7.46-9.65	9.14-11.60
Caudal peduncle length/Peduncle depth	1.54-2.08	1.31-1.69
Pre-dorsal length/Standard length	0.73-0.78	0.74-0.79
Standard length/Dorsal fin base length	10.90-13.86	8.00-11.78
Dorsal fin length/Fin base length	1.38-1.71	1.29-1.64
Standard length/Anal fin base length	6.44-7.68	6.02-8.20
Anal fin length/Fin base length	1.11-1.33	1.15-1.33
Pre-pelvic length/Standard length	0.53-0.56	0.49-0.56
Pectoral-pelvic length/Standard length	0.28-0.33	0.28-0.33
Pectoral fin length/Pectoral-pelvic length	0.32-0.42	0.36-0.43
Pelvic-anal length/Standard length	0.20-0.24	0.22-0.27
Pelvic fin length/Pelvic anal length	0.41-0.50	0.36-0.43
Standard length/Head length	3.92-4.39	4.06-4.54
Head length/Head width	1.87-2.14	1.87-2.29
Head length/Inter-orbital width	3.01-3.50	2.67-3.25
Head length/Eye diameter	3.67-4.50	3.72-4.58
Head length/Gape width	3.29-4.00	2.90-3.80

B R E V I O R A

Museum of Comparative Zoology

CAMBRIDGE, MASS. 6 APRIL, 1967 NUMBER 266

A NEW SPECIES OF *VESICOMYA* FROM THE CARIBBEAN SEA (MOLLUSCA: BIVALVIA: VESICOMYIDAE)

By

Kenneth Jay Boss

Museum of Comparative Zoology
Harvard University

During Cruise 104 (fall 1965) of the M/V OREGON of the Bureau of Commercial Fisheries Pascagoula Fishery Station, Pascagoula, Mississippi, an unusually large bivalve was trawled, alive, from a depth of over two hundred fathoms (366 m) off the coast of Colombia in the Caribbean Sea. Upon examination and comparison with material in the United States National Museum, the specimen was found to be referable to the rare and enigmatic family Vesicomyidae. The unique specimen is not conspecific with any known species of this family and is herein described as new.

VESICOMYA (CALLOGONIA) CARIBBEA sp. nov.
Figures 1-6

Holotype: Division of Mollusks, U. S. National Museum, catalog number 674573.

Type locality: M/V OREGON Station 5692, 12°31′N; 70°58′W; 205 fathoms (375 m); Caribbean Sea, off Cabo la Vela, Peninsula de Guajira, Colombia; bottom temperature 55°F (12.8°C); 10 October 1965. The specimen was collected alive by a 40′ shrimp trawl.

Description: Shell 96 mm long, 67 mm high and 54 mm wide, irregularly elliptical, inequilateral, equivalve, solid, frangible, inflated with both valves of equal convexity, without posterior gape, but with slight undulate flexure to right posteriorly. Umbos anterior, conspicuous, involute, pointed, prosocline, slightly elevated

and inflated; umbonal cavity deep. Anterior margin not extensive, very broadly rounded and weakly convex; ventral margin extensive, weakly convex, rising gently posteriorly; anterior dorsal margin short, semisigmoid, concave umbonally, rounded and convex distally; posterior dorsal margin convexly arcuate and coextensive with posterior margin, forming broad blunt, oblique truncation; outline weakly pointed posteroventrally. Sculpture closely set, fine concentric laminae, grouped between larger, more conspicuous, irregular growth rings; radial sculpture not evident. Posterior ridge, semisulcated dorsally, radiating from umbo toward posteroventral region, becoming weaker distally. Ligament strong, protuberant, black, elongate, lanceolate, slightly inset basally, supported by thickened hinge line, and forming broad elongate nymph. Lunule not developed or circumscribed by impressed isocardioform line. Hinge dentition invested with periostracum. Right valve with two cardinal teeth beneath umbo; ventral tooth stronger and protuberant; dorsal tooth with anterior laminar portion and posterior thickened portion. Left valve with single central cardinal tooth developed, strong and protuberant; anterior laminate portion broken and obsolete; secondary laminate tooth beneath umbo broken. No true internal radial rib, but rib-like thickening present on posterodorsal margin of anterior adductor muscle scar. Muscle scars moderately impressed, large, irregularly ovate, anterior smaller than posterior. Pallial line weakly convex; pallial sinus irregular, narrow; pallial line not directly or obviously contiguous with posterior adductor muscle scar. Internal surface of valve with radial vermiculations. Periostracum dehiscent, olivaceous, wrinkled, heavier peripherally, also thickened over cardinal and anterior portions of hinge internally. Shell basically white, externally grayish to olivaceous, discolored centrally with russet band; earthy and chalky in texture; internally shining, with darkened blotches and pale salmon centrally.

Remarks: The family Vesicomyidae (originally spelled Vesicomyacidae) was established by Dall and Simpson (1901). It has been reviewed by Lamy (1920), and recently Odhner (1960) has listed the species referable to *Vesicomya*. The status of the family has been questioned: Thiele (1935), Odhner (1960) and Clarke (1962) included *Vesicomya* in the Kellyellidae. Jukes-Browne (1913) even mentioned it in relation to the Veneridae. On the other hand, Dall (1908), Thiele and Jaeckel (1931), Prashad (1932), Taki and Habe (1955), and Newell (1965) have maintained the Vesicomyidae separately.

There is also a question as to what genera should be included in the Vesicomyidae. For example, Woodring (1938) placed *Calyptogena* Dall, along with his newly described genera *Ectenagena* and *Phreagena,* in the Vesicomyidae. An historical survey of the family and a critical revision of at least the western Atlantic species is currently being prepared.

No western Atlantic *Vesicomya* approaches the size of *V. caribbea. V. leeana* (Dall, 1889, p. 440; 1890, pl. 10, figs. 6-9) is the only western Atlantic species that is closely related to and which might be confused with *V. caribbea.* The latter is easily distinguished by being much larger and having a heavier shell with a distinct posterior ridge. In addition, the hinged teeth of *V. caribbea* are stronger and more blunt. The eastern Pacific species, *V. gigas* (Dall, 1896, pl. 18; 1908, pl. 16, fig. 9), attains the size of *V. caribbea* but it is usually less heavily shelled and its teeth are more distinct. It may be differentiated from *V. caribbea* by its much shorter ligament and shorter, more distinct, nymphal callosity. Further, *V. gigas* lacks a posterior ridge and is generally of longer, narrower proportions. Also, *V. gigas* is mesially constricted ventrally while *V. caribbea* is not.

The two species most closely related to *V. caribbea* are known only from widely separated localities and are also rare in collections. The most closely related is *Vesicomya chuni* described by Thiele and Jaeckel (1931, p. 244, pl. 4, fig. 100) from VALDIVIA Station 63, 2° N; 8°4.3′E, from a depth of 2492 m in the Gulf of Guinea, eastern Atlantic Ocean. Unfortunately, the authors did not figure an internal view of the shell and no specimens of this species were available for comparison. The outline of the valves of *V. caribbea* and *V. chuni* are quite similar; however, the semisulcated posterior ridge of *V. caribbea* appears to be a distinguishing character. Further, according to Thiele and Jaeckel's description, *V. chuni* is relatively thin shelled, whereas *V. caribbea* is thick shelled.

The other species closely resembling *V. caribbea* is from the East Indian area. *Vesicomya winckworthi,* described by Prashad (1932, p. 153, pl. 5, figs. 7-8) from SIBOGA Station 17, 7° 28.5′S; 115°28′E, in 1060 m depth, north of Java, is founded on a single right valve which, fortunately, was well illustrated externally and internally. In contrast to *V. winckworthi, V. caribbea* is apparently more inflated, its anterior margin more narrowly rounded, and its nymph stronger and thicker.

Vesicomya caribbea is placed in the subgenus *Callogonia* Dall 1889 (type-species, by monotypy, *Callocardia* [*Vesicomya*] *leeana*

Dall 1889), as its pallial sinus is, though indistinct, somewhat angular. Thiele and Jaeckel (1931) placed *V. chuni,* the species most closely related to *V. caribbea,* in *Callogonia.*

ACKNOWLEDGMENTS

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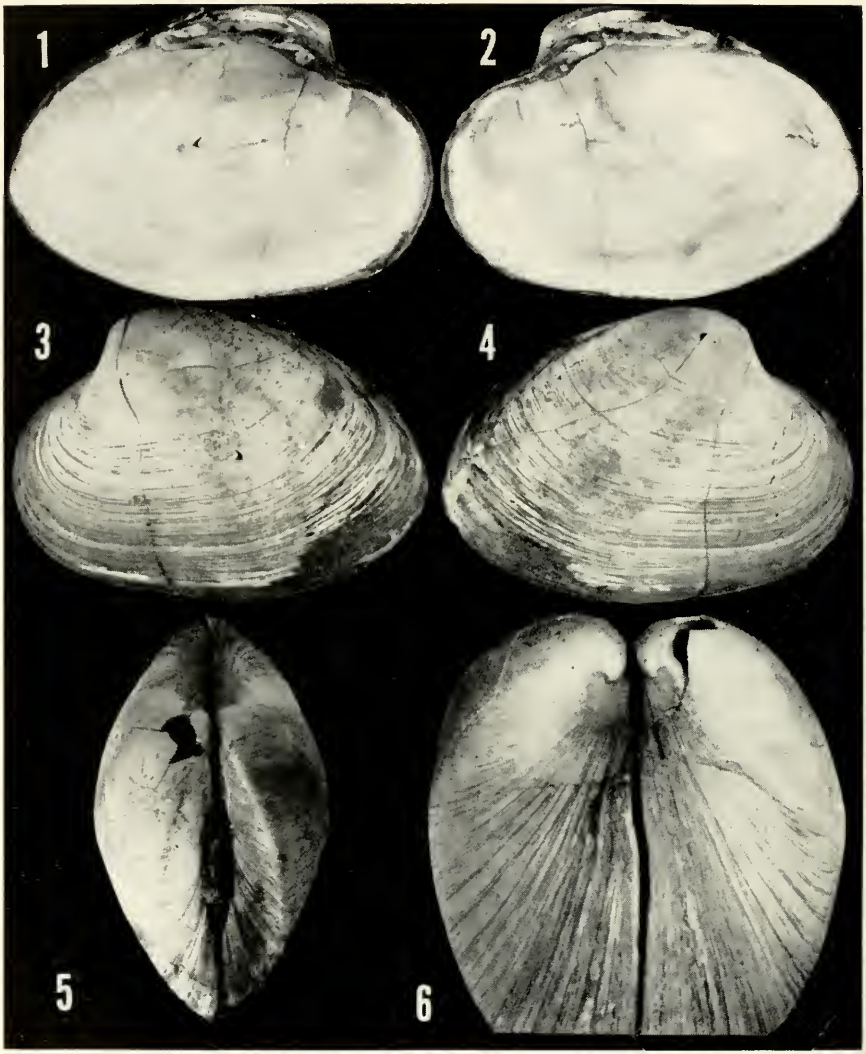

Vesicomya (*Callogonia*) *caribbea* n.sp., Holotype, USNM 674573.

Fig. 1. Internal view of left valve. Fig. 2. Internal view of right valve. Fig 3. External view of left valve. Fig. 4. External view of right valve. Fig. 5. Dorsal view of valves, showing posterior ridge. Fig. 6. Anterior view, showing involute umbos.

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A NEW GENERIC ARRANGEMENT FOR SOME AUSTRALIAN SCINCID LIZARDS

By Allen E. Greer

In Boulenger's (1887, vol. 3) classification of skinks, the genus *Lygosoma* was by far the largest and most heterogeneous group that defied further splitting on the basis of the characters used. Unable to recognize "natural" distinctions which would warrant full generic rank, Boulenger designated 11 "natural" species groups of *Lygosoma* as subgenera and thereby established a ranking system that then, as now, was little used in lizard taxonomy.

The relationships of one of Boulenger's *Lygosoma* subgenera, the subgenus *Rhodona,* and part of the genus *Ablepharus* are re-examined in the present paper.

Boulenger's (1887:223) subgenus *Rhodona* was based on an unusually large suite of external characters, being defined as follows: "Limbs short or rudimentary. Lower eyelid with a transparent disk. Ear distinct, minute. No supranasals. Praefrontals very small and widely separated, or absent. Frontal broader than the supraocular region."

To this list could have been added the following: nasals enlarged so that they just fail to touch or do touch medially, 2-5 pairs of nuchals, and a single pair of enlarged preanals. In addition, it might have been noted that the group is found only in Australia and Tasmania.

The widespread Old World genus *Ablepharus,* on the other hand, was based essentially on a single character, Boulenger (1887: 344) including in this genus all those skinks lacking "movable eyelids" and with a "transparent disk covering the eye." Obviously, Boulenger in this instance put great confidence in a single character, the "ablepharine" eye.

This single character approach should not be thought of as being too incongruous with Boulenger's general philosophy. In most other reptile groups with the "ablepharine" eye (non-eublepharine geckos, pygopodids, xantusids, and snakes), the character was

then and may still be rightly regarded as the hallmark of natural taxa. The "ablepharine" skinks, however, are an exception.

Boulenger's basic conception of *Rhodona* and *Ablepharus* was accepted by the authors of the two subsequent revisions of the "lygosomine" skinks (Smith, 1937; Mittleman, 1952). Malcolm Smith (1937) gave *Rhodona* full generic rank and included within it three southeast Asian (*anguinoides, roulei,* and *gyldenstolpei*) and one Australian (*australis*) species that in 1935 he had considered the sole representatives of the genus *Ophioscincus.*[1] This arrangement, however, was suspect on two counts. First, the species of *Ophioscincus* differ from those of *Rhodona* in lacking both fore and hind limbs and external ear openings, and in having no or only one pair of nuchals, and second, such an arrangement involves an improbable geographic distribution.

All skinks with an immovable transparent disc covering the eye were retained in *Ablepharus* by Smith (1937). In this he followed Boulenger, although he noted in 1935 that the group was almost certainly polyphyletic, probably having arisen from *Leiolopisma* and *Emoia* stocks.

Mittleman (1952), taking his cue from Smith's reasonable supposition of the polyphyletic nature of *Ablepharus,* cut the Gordian knot by separating out all *Ablepharus* that had the frontoparietals and interparietal fused into a single scale and placing them in the genus *Cryptoblepharus.* It is interesting to note that the "ablepharine" eye was still sacrosanct; no "ablepharine" skink was lumped with a non-"ablepharine" skink.

Similarly, Mittleman split Boulenger's *Rhodona* into two genera: *Rhodona* with the frontoparietals and interparietal fused into a single scale (indicated as 1 in Table 2), and *Nodorha* in which the frontoparietals are distinct (2/1) or fused (1/1) but always distinct from the interparietal.

Mittleman removed the four species of *Ophioscincus* from the *Rhodona-Nodorha* complex and was certainly right in doing so. However, in reverting to Smith's 1935 treatment of the genus *Ophioscincus,* he has re-emphasized the anomalous geographic distribution of that genus. The disjunct Australian, southeast Asian distribution, once again, makes the "naturalness" of the genus suspect.

Although Mittleman's arrangement provides groupings which are of value in identifying and cataloging skinks, it fails to demonstrate

[1] In 1887 the only known species of *Ophioscincus* Peters, 1873 was *australis,* and this was put in the subgenus *Lygosoma* by Boulenger.

any greater awareness for the evolution of higher taxa than did earlier pre-Boulengerian classifications. This has been an *a priori* criticism of Mittleman's lygosomine classification since its publication, and perhaps explains why his system has been passed over in favor of a Boulenger-Smith arrangement by most present day authors. Even these two earlier authors must have been aware of many of Mittleman's "generic characters" but chose not to use them.

In my own research on the higher taxa of the skinks I have attempted to correlate characters of external morphology and skull morphology. It is my contention that when a suite of external and skull characters can be found in only a certain group of species, there is strong evidence that the group is "natural," i.e., monophyletic. The geographic distribution of the taxon is used as a further check of the validity of the arrangement. If the distribution of the taxon is consonant with the general geographic barriers influencing the distribtuions of other taxa, then the argument for the validity of the new taxon is strengthened.

A consideration of the external morphology has, of course, been the standard approach in skink taxonomy, although, like Boulenger (1887:131), I believe I have found new characters which are important.

Little has been done with skull morphology in relation to skink classification. Boulenger examined the relationships of the bones of the palate as seen through the epidermis of the mouth and utilized what he saw at the generic level. This method led to some serious misinterpretations of the anatomical facts and these have been perpetuated (see Smith, 1935, and Mittleman, 1952, for example) until the present time. By removing the epidermis overlying the palate, Waite (1929) and Mitchell (1950) made a technical advance, but failed to take full advantage of it in their own taxonomic work.

My own approach (outlined above) has provided evidence which convinces me of the previously only suspected polyphyletic nature of many groupings in all three earlier classifications (Boulenger, 1887; Smith, 1937; and Mittleman, 1952). Many of the single characters which were utilized exclusively or heavily in diagnosing skink taxa simply do not correlate with any other characters (internal or external), as one would expect them to do in a natural group.

Other correlations utilizing skull and external characters are possible, however, and will form the basis of a new classification of skinks. This brief study delimiting a newly recognized taxon and giving it generic rank is an example of the new approach and

is a first contribution toward the distant goal of a complete generic revision of the skinks.

The taxon to be discussed here consists of all the species of *Rhodona* (*sensu* Boulenger) and those species of Australian *Ablepharus* that conform to the descriptions of *Rhodona* except for the "ablepharine" eye (Table 2). The earliest named species of the group (*Ablepharus lineata*) was described by Bell in 1833 (see below) as the type species of *Lerista.* The new taxon should therefore be properly known as *Lerista,* with the following primary generic synonymy.

Lerista Bell

Lerista Bell, 1883, Proc. Zool. Soc. London, p. 99 (Type species, *Lerista lineata* Bell, 1833, by monotypy)

Rhodona Gray, 1839, Ann. Mag. Nat. Hist., vol. 2, p. 335 (Type species, *Rhodona punctata* Gray, 1839, by monotypy).

Soridia Gray, 1839, Ann. Mag. Nat. Hist., vol. 2, p. 335 (Type species, *Soridia lineata* Gray, 1839, by monotypy).

Brachystopus Duméril and Bibron, 1839, Erpétologie générale, vol. 5, p. 778 (Type species, *Brachystopus lineopunctulatus* Duméril and Bibron, 1839 = *Rhodona punctata* Gray, 1839, by monotypy).

Praepeditus Duméril and Bibron, 1839, Erpétologie générale, vol. 5, p. 787 (Type species, *Soridia lineata* Gray, 1839, by monotypy).

Ronia Gray, 1841, Ann. Mag. Nat. Hist., vol. 7, p. 87 (Type species, *Ronia catenulata* Gray, 1841 = *Rhodona punctata* Gray, 1839, by monotypy).

Leptosoma Fitzinger, 1843, System reptilium, p. 23 (Type species, *Riopa bougainvillii* Duméril and Bibron, 1839, by monotypy).

Ophiopsis Fitzinger, 1843, Systema reptilium, p. 23 (Type species, *Lerista lineata* Bell, 1833, by monotypy).

Miculia Gray, 1845, Catalogue of the specimens of lizards in the collection of the British Museum, p. 66 (Type species, *Miculia elegans* Gray, 1845, by monotypy).

Pholeophilus A. Smith, 1849, Illustrations of the zoology of South Africa, p. 15 of Appendix (Type species, *Pholeophilus capensis* Smith, 1849 = *Soridia lineata* Gray, 1839, by monotypy).

Phaneropus Fischer, 1881, Arch. Naturg. Jhrg. 47, p. 236 (Type species, *Phaneropus muelleri* Fischer, 1881, by monotypy).

Nodorha Mittleman, 1952, Smithsonian Misc. Coll., vol. 17, p. 14 (Type species, *Riopa bougainvillii* Duméril and Bibron, 1839, by original designation).

DIAGNOSIS OF THE GENUS *LERISTA*

There is no single diagnostic character that will distinguish the species of *Lerista* from all other skink taxa. This is, however, not

to say that once one is familiar with the diversity of skinks that a species of *Lerista* cannot be identified as such at a glance.

On the basis of external characters, the taxon may be diagnosed as follows: no supranasals; nasals enlarged so that they just fail to touch or do touch medially; prefrontals reduced and widely separated or absent; frontal generally broader than supraocular region; frontoparietal/interparietal configuration = 2/1, 1/1, or 1; 2-5 pairs of nuchals; lower eyelid with a transparent disc and either movable or fused to form a permanent spectacle; no row of scales separating the small scales of the eyelid from the subocular supralabial; ear opening small to minute, but always present; a single pair of enlarged preanals; body form attenuate; limbs diminutive or rudimentary, but never totally lacking (digital formula from 5-5 to 0-1).

DESCRIPTION AND RELATIONSHIPS OF THE GENUS *LERISTA*

The following description of the taxon *Lerista* is based on an examination of whole skulls, alcoholic specimens (see Materials section of paper), and also of type descriptions when species have not been available.

The skull is considered first, as skull morphology has generally proved more useful in determining the broader relationships of skinks than has external morphology.

Skull morphology: The skull characters of the species are remarkably uniform, although the species adapted to a more burrowing way of life (e.g., *L. bipes* and *L. praepedita*) show certain modifications in the skull that are often seen in burrowing skinks.

To facilitate comparisons with its near relatives, a brief description of the skull characters of the genus is given.

The whole skull tends to be somewhat conical in shape. The palatines are approximately 2-2½ times as long as broad and meet along their entire medial edge. The palatal rami of the pterygoids are "squared-off" and in some species slightly emarginate posteriorly, and they also meet along their medial edge (Fig. 1). The palatines and palatal rami of the pterygoids thus form an extensive "secondary palate." Among lizards the tendency toward the formation of a bony secondary palate is unique to skinks, and the extensive palatine-pterygoid palate of *Lerista* is, in turn, a rather "advanced" development of the palate in skinks.

An ectopterygoid process extends forward along the lateral edge of the palatal ramus of the pterygoid, past the palatine-pterygoid suture and onto the posterolateral edge of the palatine, thereby

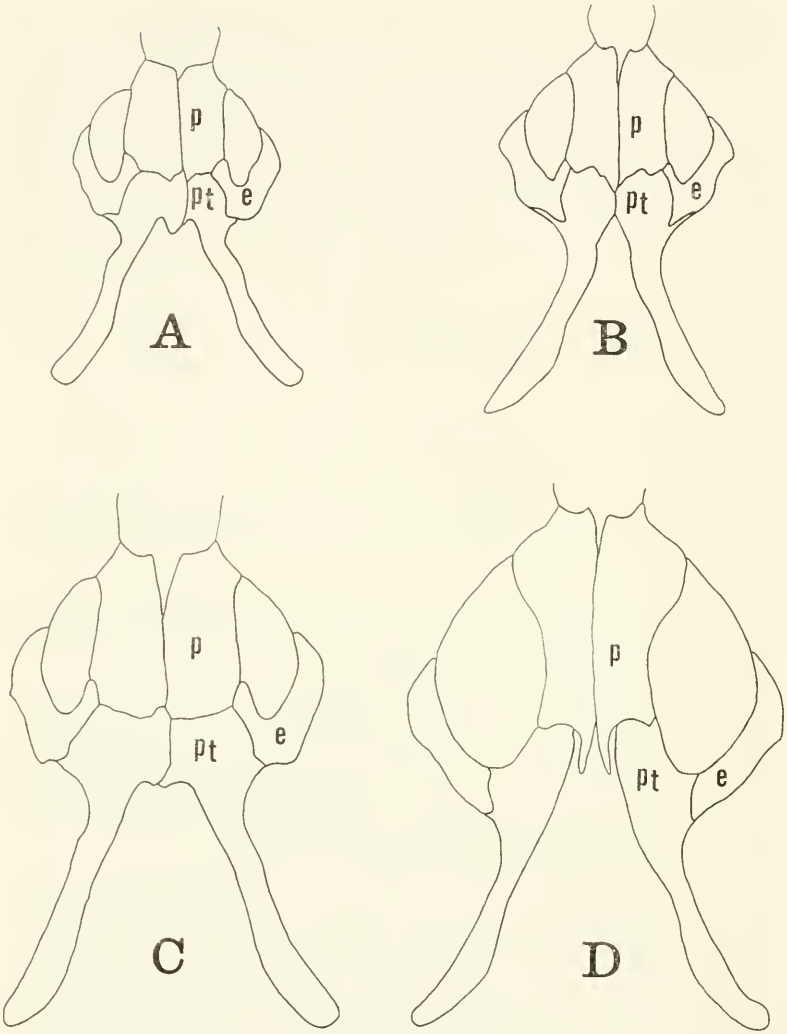

Figure 1. Ventral view of the palate of *A, Lerista elegans* (FMNH 11319), Lake Toolburnup (= Tool Brumup), Western Australia; *B, Sphenomorphus pardalis* (MCZ 35413), Coen, Cape York, Queensland; *C, Lerista bougainvilli* (MCZ 61403), Tallarock, Victoria; *D, "Ablepharus" lineo-ocellatus* (MCZ 33144), Margaret River, Western Australia. Abbreviations for this figure: *e,* ectopterygoid; *p,* palatine; *pt,* pterygoid, *A, C,* and *D* drawn to scale.

excluding the pterygoid from a position on the infraorbital fenestra (Fig. 1). This anteriorly projecting ectopterygoid process is also unique to skinks, among lizards, although it is not found in all skinks.

The premaxillae and nasals are paired; the vomer, frontal, and parietal are single. There is a parietal foramen in the parietal. The frontal and maxilla form a surface suture or the frontal, prefontal, maxilla, and nasal meet at a point.

The temporal arch and the postorbital bar (formed by the jugal) are present. A small supratemporal fenestra may be present but is more frequently covered by the posterior extension of the postfrontal. A postorbital is lacking.

The bones of the skull and mandible generally lack pigment.

Teeth are present on the maxillae, premaxillae, and dentaries. There are usually 7 (5 in *L. bipes* and 6 in *L. lineopunctulata*) teeth on the premaxillae and 9-13 (usually 11-12) on each maxilla.

Meckel's groove may be present or partially overlapped by the dentary.

Relationships as inferred from skull morphology. On the basis of the relationships of the bones of the palate, *Lerista* is most similar to *Hemiergis* and one group of *Sphenomorphus* species (Fig. 1). For convenience, this latter group may be referred to as the *solomonis* group; it encompasses so far as is known the following species: *solomonis, emigrans, pardalis, australe, antimorum, crassicauda, tenuis,* and *tryoni.* The species of all three groups, that is *Lerista, Hemiergis,* and the *solomonis* group, have the palatines and the pterygoids meeting along the midline, and, except for three species of *Hemiergis* and *S. australe,* the species of all three groups possess an ectopterygoid process which extends forward to the palatine to exclude the pterygoid from the infraorbital vacuity.

In *Hemiergis peroni, H. tridactylus,* and *H. initiale* the anteriorly projecting ectopterygoid process has been secondarily reduced to a small nubbin which fails to exclude the palatal ramus of the pterygoid from a position on the infraorbital vacuity. The process is better developed in *S. australe* where it extends anteriorly about half way along that outer edge of the palatal ramus that would, in the absence of the process, border the infraorbital fenestra.

The species of the genus *Hemiergis* and the *solomonis* group, however, differ from the *Lerista* skinks in possessing more teeth on the premaxillae (8-9) and in having a long thin postorbital.[1]

[1] The number of teeth on the premaxillae and the absence or presence and shape of the postorbital are of greater taxonomic significance in skinks than in most other lizard families.

The relationship of the bones of the palate described above for *Lerista* and its near relatives is not found in any *Ablepharus* other than in the "ablepharine" *Lerista*. In all other *Ablepharus* the palatal rami of the pterygoids are separated (contrary to Boulenger's 1887 diagnosis of the genus), and there is no ectopterygoid process (Fig. 1).

Furthermore, in all *Ablepharus* other than the "ablepharine" *Lerista* there are usually 9 (or more) teeth on the premaxillae, and the prefrontal often forms a broad suture with the nasal.

External morphology: In gross aspect the species of *Lerista* are attenuate skinks in which the tail comprises fully half the total length. The appendages are diminutive and widely separated when adpressed to the body. The head tends to be somewhat conical to wedge shaped.

Upon closer inspection it can be seen that the nasals are enlarged in a dorsoventral aspect so that they meet mid-dorsally behind the rostral or just fail to do so.

There are no supranasals and the frontonasal is wider than long. The prefrontals are small and widely separated or, in some species, they are absent. The frontal tends to be wider than the supraocular region and is in contact with 1 or 2 (usually 2) of the 2 to 4 (usually 3) supraoculars.

The frontoparietals and interparietal display the three possible degrees of fusion. The degree of fusion is indicated in Table 2 by a simple notation in which the number of frontoparietals is given on the left side of the slash mark (/) and the interparietal is indicated on the right side. The numeral one means that all three scales are fused into a single scale.

It can be seen from the data in Table 2 that there is a very approximate correlation between the state of fusion of the frontoparietals and interparietal and the reduction of the appendages and digits. Reduction of the appendages and digits is in turn correlated with burrowing habits. It would appear, therefore, that in species of more burrowing habits there is a greater tendency for the frontoparietals and interparietal to fuse. This is just one of several evolutionary trends (see below) in the group and, to me, it seems pointless to break the concept of this trend by splitting the spectrum into two parts as Mittleman (1952) did when he set up *Nodorha* as distinct from *Rhodona*.

The parietals meet behind the interparietal, and there are 2-4 pairs of nuchals.

There is a well defined transparent area or "window" in the lower

eyelid. In most species the lower eyelid is movable, but in a few it has become fused to the upper resulting in an "ablepharine" eye (Table 2). In all species of *Lerista* a supralabial contacts the small scales of the lower eyelid below the transparent area and thereby acts as a subocular. There are 2-4 (usually 3) supralabials anterior to the subocular (= a supralabial).

The external ear opening is small, that is, it is smaller than the transparent area in the lower eyelid, but although the opening is minute in several species, it is never completely covered over by the epidermis.

The scales around the midbody are smooth and number 16-24. There is a pair of very large preanals. The three midventral series of subcaudals are subequal.

The digital formula (fingers-toes) ranges from 5-5 to 0-1 (Table 2). Only two species have 5-5 while all others show a reduced number of digits, although no species is limbless. The digits are covered above by a single row of scales (Group I of Brongersma, 1942).

Color patterns in the genus are variations on a striped motif (Table 2). A solid, dark, dorsolateral stripe is common and often occurs in conjunction with either a third mid-dorsal dark stripe or with a pair of mid-dorsal broken dashed stripes on the two dorsalmost scale rows. A few species, on the other hand, lack broad dorsolateral or mid-dorsal stripes and simply have broken dashed stripes on each dorsal scale row. There seems to be little intraspecific variation in regard to pattern type.

In addition to the osteological differences mentioned above, two features of the external morphology serve to further separate the "ablepharine" *Lerista* from other *Ablepharus* and unite them with *Rhodona* in a common genus. These are (1) the enlarged nasals and (2) the reduced number of digits. Of all other *Ablepharus* only *A. greyi* and *A. burnetti* have a reduced number of digits (4-5). These two Australian species are, however, only distantly related to *Lerista* and will be discussed at a later date.

It might also be mentioned here that the species of *Lerista* differ from those attenuate, burrowing skinks of the subgenus *Lygosoma* which occur in Australia in having transparent eyelids and external ear openings rather than having scaly eyelids and completely covered ear openings.

The differences in skull morphology between *Lerista, Hemiergis* and the *solomonis* species group have been mentioned above.

Table 1 summarizes the external differences between the three groups.

Geographic distribution of Lerista and its relatives: It is significant that the genus *Lerista* is found only in Australia and Tasmania. If we discount, for reasons given above, any close affinity with *Ablepharus* and *Ophioscincus,* then it is clear that there are no close relatives of *Lerista* in either Africa or Eurasia.

The closest relatives of *Lerista,* namely *Hemiergis* and the *solomonis* assemblage, are quite obviously a product of the Australian Region. The species of *Lerista* represent an exclusively Australian adaptive radiation into the "surface litter and subsurface burrowing niche." They are certainly not the only lizards to have entered this niche — *Hemiergis* and some of the *solomonis* group species mentioned above also occupy it — but *Lerista* is one of the most successful groups to exploit it, if diversity and abundance are criteria for such success. Furthermore, it is the most specialized species of this genus that have exploited the relatively new (geologically speaking) arid areas of Australia.

EVOLUTIONARY TRENDS WITHIN THE GENUS *LERISTA*

The species of the genus as it is understood here can be arranged according to certain structural sequences that are undoubtedly indicative of the evolutionary trends that have occurred within the group.

One of these trends has been a reduction in the size of the limbs and the number of digits on the fore and hind feet (Table 2). In this regard it should be noted that the number of digits on the forefront are equal to or less than, but never greater than, the number of digits on the hindfoot. This pattern of digit reduction is common among lizards, the most noteworthy exceptions being the amphisbaenid *Bipes biporus* (digital formula = 5-0) and the scincid genus *Ophiomorus.* In the latter genus the number of fingers is equal to or greater than, but never less than the number of toes (Anderson and Leviton, 1966).

The reduction of the digits in *Lerista* is not unexpectedly correlated with other structural changes indicative of greater adaptation to burrowing habits (Mitchell, 1958); e.g., the size of the eye is reduced somewhat, the lower jaw becomes more countersunk into the upper, and the ear openings become more minute but never disappear.

Although there is a tendency toward smaller external ear openings in the species of *Lerista* more closely adapted to a burrowing

existence (e.g., *L. bipes* and *L. praepedita*), the quadrate bone undergoes no striking changes in shape from that found in most lizards with external ear openings. The bone is excavated posteriorly, and the tympanum attaches to the lateral rim. By way of comparison, the five species of *Hemiergis* are less closely adapted to a fossorial life than many of the *Lerista* skinks but have developed a simple rod-shaped quadrate concomitant with the loss of the external ear opening.

Several characteristic changes in the skull are found in the extreme burrowers of the group (*L. bipes* and *L. praepedita*). The skull posterior to the orbits is proportionately elongated, and the supra- and post-temporal fenestrae are often completely closed over, although no elements in the arches are lost. The prefrontal also tends to be reduced in its anterior extension, and posteriorly may touch the postfrontal to exclude the frontal from the orbit. In *L. bipes* and *L. praepedita* the premaxillae project forward well beyond the level of the premaxillary teeth, a modification which is undoubtedly an advantage to these species which employ the snout as a burrowing wedge.

The very approximate correlation between the loss of digits and the fusion of the frontoparietals and the interparietal (Table 2) has already been mentioned.

Most of the species of *Lerista* that have followed these trends to the extreme are among Australia's most closely adapted arid area dwellers. In this regard they are to arid Australia what *Ophiomorus* and *Scincus* are to arid southwest Asia and North Africa. The similarities are, of course, entirely convergent, for *Ophiomorus* and *Scincus,* which are rather closely related, are fairly distantly related to *Lerista.*

MODE OF REPRODUCTION IN *LERISTA*

Nothing has been published concerning the breeding habits of these skinks, although from the meager data presented below, it is evident that there are both live-bearing and egg-laying species in the genus.

A single *Lerista microtis* (MCZ 24577) with a snout-vent length of 51 mm contains three young in which scales and color pattern are evident, indicating that the young would probably be born.

L. timida, on the other hand, is apparently oviparous. A gravid female (snout-vent length = 40 mm) in the Field Museum of Natural History (97739) contains two oblong, whitish, leathery shelled eggs. An untagged female (snout-vent length = 46 mm) in the MCZ collection is likewise gravid with two shelled eggs.

Single females of *L. bougainvilli* (MCZ 6751; snout-vent length = 60 mm) and *L. punctatovittata* (FMNH 97747; snout-vent length = 85 mm) each contain three spherical, yolky oviducal eggs. These eggs were not far enough along in their development to allow speculation as to the mode of reproduction in either species.

THE SPECIES OF *LERISTA*

Although a thorough revision of the species in the genus is sorely needed, the following table (Table 2) may be of some use to those faced with the tedious curatorial duties of identifying and organizing collections. The table makes no pretense of being a summary of a generic revision and is based solely on the species as they are currently recognized in the literature. Two characters important in species diagnoses, namely the fusion or independence of the frontoparietals and the number of digits, are in the greatest need of re-evaluation on the intraspecific level.

The number of digits is, in fact, already known to vary somewhat within a single species. Boulenger (1887:335) recorded *R. gerrardi* as having either mono- or didactyl forelimbs, and Kinghorn (1924:180) reported on a specimen of *R. punctatovittata* with the "forelimb distinctly didactyl" rather than monodactyl. Loveridge (1934:372) also found a "rudimentary stump of a second toe" in *R. miopa,* a species which had previously been considered as having only a single toe on the hind foot.

Mitchell (1955:402) studied the variation in the tarsal (carpal) and metatarsal (metacarpal) bones in nine species of *Rhodona* and came to the conclusion that "among specimens of the same species . . . from different localities . . . the loss of digits and digital bones may not be always indicative of specific variation. The genus may be found to contain polytypic species within which the number of digits varies."

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Both Dr. Williams and my wife Carol have read and criticized the manuscript in many helpful ways.

MATERIALS

Complete skulls of the following specimens of *Lerista* have been examined: *bipes* (AMNH 86089); *bougainvilli* (MCZ 61403); *elegans* (FMNH 11319; *fragilis* (CAS 77190; MCZ 42988); *gerrardi* (MCZ 33255); *lineopunctulata* (BM 1902.7.30.5); *miopa* (MCZ 33260); *muelleri* (MCZ 86699); *planiventrale* (BM 1954.1-2.21); *praepedita* (MCZ 33265); *punctatovittata* (MCZ 79494); *tetradactyla* (BM 1902.7.30.6); *timida* (MCZ x-13246).

In addition, the relationship of the palatine, palatal ramus of the pterygoid, and the ectopterygoid were examined in the following specimens of *Lerista: bipes* (MCZ 33251, 35349, 35350, 79570); *bougainvilli* (MCZ 67149); *elegans* (MCZ 33126, 33136); *tetradactyla* (MCZ 51893); *timida* (MCZ 33152, 33153).

Nineteen of the 28 species of *Lerista* were available for examination as alcoholic specimens: *allanae* (2); *bipes* (20); *bougainvilli* (20); *distinguenda* (1); *elegans* (17); *fragilis* (many); *gerrardi* (12); *lineata* (2); *lineopunctulata* (1); *microtis* (2); *miopa* (3); *muelleri* (18); *nichollsi* (1); *planiventrale* (2); *praepedita* (6); *punctatovittata* (24); *stylis* (1); *tetradactyla* (6); *timida* (20).

For comparative purposes the following skulls of *Lerista's* near relatives were examined: *Hemiergis decresiensis* (MCZ 49173); *H. initiale* (MCZ 33210); *H. peroni* (MCZ 24648, 24652); *H. quadrilineatum* (MCZ 33210); *H. tridactylum* (MCZ 24595).

Sphenomorphus antimorum (MCZ 25374); *S. australe* (MCZ 24568); *S. crassicauda* (AMNH 82606); *S. emigrans* (MCZ 27043); *S. pardalis* (MCZ 35413); *S. tenuis* (MCZ 35398); *S. tryoni* (MCZ 35387; 35388); *S. solomonis* (MCZ 72618, 72626, 72664, 72665, 77373, 77374).

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TABLE 1

The differences in external characters between the genus *Lerista* and the two groups most closely related to it.

	Lerista (28 species)	*Hemiergis* (5 species)	*solomonis* group (8 species)
Nasals	Proportionately enlarged	Not so.	Not so.
Digital formula	2 species with 5-5; all others with 4-4 to 0-1.	1 species with 5-5; all others with 4-4 to 2-2.	All species with 5-5.
External ear opening	Present but small to minute.	Absent, indicated by a depression.	Large, well defined.
Lower eyelid	With a clear "window."	With a clear "window."	Scaly.
Supraoculars	2-4 (usually 3).	Always 4.	Always 4.
Frontoparietals/ interparietal	2/1, 1/1, 1	2/1, except in *H. initiale* which has 1/1.	2/1
Supradigital scales (4th toe)	Series of single scales.	Series of paired scales.	Series of two or more scales.
Subocular scale row	Incomplete, supralabial borders small scales of eyelid throughout most of its length.	Complete, except in *H. initiale* in which the upper posterior half of the supralabial borders the small scales of the eyelid.	Incomplete, upper posterior half of supralabial borders small scales of eyelid.

TABLE 2

The species of *Lerista* with a summary of some of their diagnostic characters and distribution.

	Condition of eye	Digital formula	Frontoparietals/ interparietal	Color pattern	Distribution
*microtis** (Gray, 1845)	R[1]	5-5	2/1	White lateral stripe bordered above and below by a black stripe.	South Western Australia and South Australia.
*bougainvilli** (Duméril and Bibron, 1839)	R	5-5	2/1	Black lateral stripe.	South Australia and Victoria.
*tetradactyla** (Lucas and Frost, 1895)	R	4-4	2/1	Blackish lateral stripe, lower edge of which is hardly distinct from darker ground color of sides.	Northern Territory and South Australia.
*elegans** (Gray, 1845)	A	4-4	2/1	Black lateral band edged below with a narrow white line.	Far western Australia.
*distinguenda** (Werner, 1910)	A	4-4	2/1	Similar to *elegans*.	Far southwestern Australia.
orientalis (de Vis, 1888)	A	4-4	2/1	Flanks blackish, well defined above, below passing into smooth buff of venter.	Northwest Queensland and Groote Eyelandt, Northern Territory.

[1] The species which I have examined as alcoholics are indicated by an asterisk(*). Under the heading "condition of eye," an R indicates a movable eyelid, and an A indicates an "ablepharine" eye; that is, there is a permanent spectacle covering the eye.

terdigitata (Parker, 1926)	R	3-3	2/1	Well defined dark dorsolateral band.	Nuyt's Archipelago and the Investigator Group.
*fragilis** (Günther, 1876)	R	3-3	1/1	Sides blackish, the color being more sharply defined posteriorly.	Queensland.
*muelleri** (Fischer, 1881)	A	3-3	2/1	Dark lateral band.	Far west central Australia.
*timida** (de Vis, 1887)	A	3-3	1/1	Black dorsolateral band.	South central Queensland south to Victoria and west through central Australia to far western Australia.
*planiventralis** (Lucas and Frost, 1902)	R	2-3	2/1	Dark dorsolateral stripe.	Central Northern Territory and western South Australia west to central Western Australia.
goerlingi (Ahl, 1935)	R	2-3	1/1	Dark dorsolateral stripe.	Known only from the type locality: Marloo Station, Wurarga, Western Australia.
macropisthopa (Werner, 1903)	R	2-3	2/1	Brown color of dorsum fades into yellowish color of venter.	Queensland.
*lineata** (Bell, 1833)	A	2-3	2/1	Dark brown lateral band.	Far southwestern Australia.

TABLE 2 (Continued)

The species of *Lerista* with a summary of some of their diagnostic characters and distribution.

	Condition of eye	Digital formula	Frontoparietals/ interparietal	Color pattern	Distribution
walkeri (Boulenger, 1891)	R	2-2	1/1	Each scale of dorsum with a black spot; spots largest on the 4th scale row from the midline.	Roebuck Bay and Condillac Island, northwestern Australia.
*gerrardi** (Gray, 1864)	R	1(2)-2	2/1	Dorsum with 3 broad, dark brown longitudinal bands.	Far southwestern Australia.
*punctatovittata** (Günther, 1867)	R	1(2)-2	2/1	Each scale of dorsum with a black spot, the spots forming 6 to 8 longitudinal rows.	Southeastern quarter of Australia and Tasmania.
picturata (Fry, 1914)	R	1("bud")-2	2/1	Dark lateral band.	Southwestern Australia.
*lineopunctulata** (Duméril and Bibron, 1839)	R	1-2	1	Each scale of dorsum with a dark brown spot.	West central coastal areas of Western Australia.
*nichollsi** (Loveridge, 1933)	R	1("bud")-2	1	Dorsum with 3 broad dark longitudinal bands.	Known only from the type locality: Dalgaranger Station, Western Australia.
*miopa** (Günther, 1867)	R	1("bud")-1(2)	1	Dorsum with 4 rows of dots.	Far west central Western Australia.

nigriceps (Glauert, 1962)	R	1("bud")-1	1	Dorsum lacks bands, head black.	Known only from the type locality: NW Cape, Western Australia.
wilkinsi (Parker, 1926)	R	0-2	2/1	Dorsal and lateral scales each with a brown dot.	Known only from the type locality: Torrens Creek, Queensland.
*bipes** (Fischer, 1882)	R	0-2	1	Dark dorsolateral stripe.	Northern Territory and South Australia west through Western Australia.
*praepedita** (Boulenger, 1887)	R	0-1	1	Dark brown lateral band.	West central coastal areas of Western Australia south to the vicinity of Perth.
*stylis** (Mitchell, 1955)	R	0-1	2/1	Dark dorsolateral stripe.	Arnhem Land and Groote Eyelandt, Northern Territory.
karlschmidti (Marx and Hosmer, 1959)	R	0-1	2/1	Many (14) narrow longitudinal dorsal and lateral stripes composed of short dashes.	Known only from the type locality: Woodstock, north central Queensland.
*allanae** (Longman, 1937)	R	0-1	2/1	Scales mostly bordered with darker markings, these dark spots forming 5 almost continuous lines on the back.	Central Queensland.

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THE ECOLOGY AND BEHAVIOR OF TWO SYMPATRIC *LYGODACTYLUS* GECKOS

Allen E. Greer

During a two-month field study (23 June-25 August 1965) of the behavior and ecology of the reptiles and amphibians of south Turkana, Kenya, data were collected on the two closely related and ecologically similar *Lygodactylus* geckos (*L. picturatus keniensis* and *L. somalicus battersbyi*) which occur sympatrically in the area.

Both species are small as geckos go. Adult *L. picturatus keniensis* Parker range in snout-vent length from about 26-35 mm and are dark grayish brown above with longitudinal light and dark markings on the head and shoulders. Adult *L. somalicus battersbyi* Pasteur are smaller, with snout-vent lengths of 21-27 mm, and are uniformly light gray to sandy beige on the dorsum. In the field it was virtually impossible to tell the sexes of either species apart solely on the basis of color pattern.

Both species, *L. picturatus keniensis* Parker and *L. somalicus battersbyi* Pasteur, are diurnal as are all the other species in the genus, although the ophthalmological evidence indicates that the group has reacquired diurnal habits from a nocturnal ancestry (Underwood, 1954:470).

As most geckos are primarily nocturnal, it is not surprising that the information which does exist on gecko behavior deals largely with the more easily observed diurnal species. Kästle's (1964) terrarium studies of *Lygodactylus p. picturatus* and three species of diurnal *Phelsuma* are among the most comprehensive available for geckos. His comparisons between these two groups of diurnal geckos should be a stimulus for obtaining more information by which the comparisons may be extended to other diurnal (e.g., *Gonatodes* and *Sphaerodactylus*) and nocturnal species.

Distribution: Lygodactylus is an African-Malagasy genus in both origin and distribution. *L. picturatus*[1] is widely distributed throughout east and central Africa and is the most widespread of the 13+

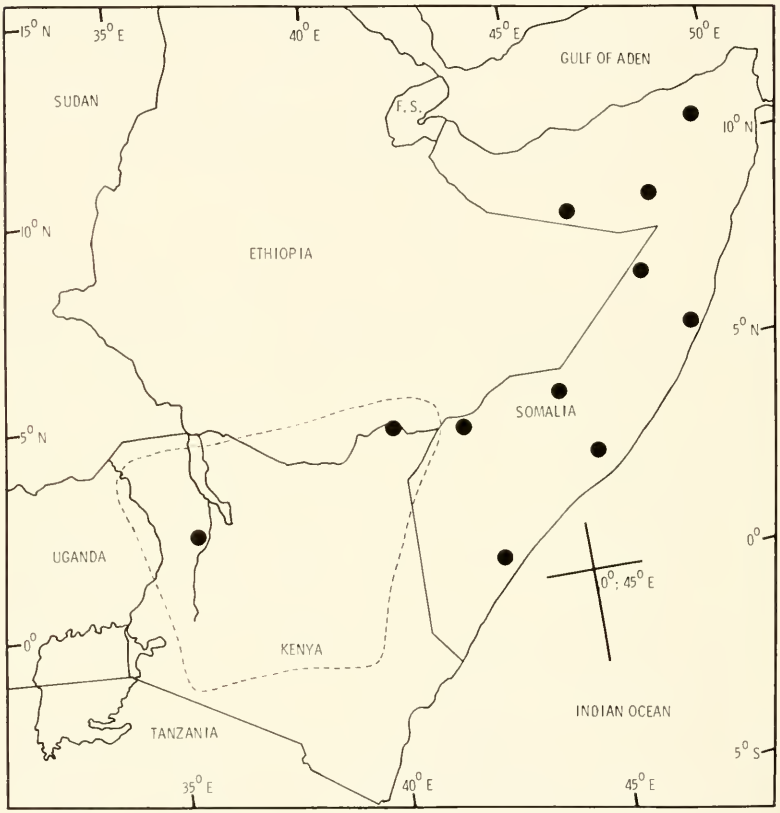

Figure 1. Map showing the distribution of *Lygodactylus picturatus keniensis* (area bounded by the dashed line), and localities outlining the distribution of *L. somalicus* (black dots). The westernmost locality for *L. somalicus* corresponds to the study area where the data for the paper were collected. *L. picturatus* (subspp.) occurs throughout the area shown in the map, except on the Arabian Peninsula. The distribution of *L. p. keniensis* is adapted from Pasteur (1964:77, fig. 20). The abbreviation F.S. stands for French Somaliland.

[1] I follow Loveridge's (1947) and Pasteur's (1960) taxonomic treatment of the genus. By simply calling *L. picturatus* a superspecies and raising subspecies to species rank, Pasteur (1964) has not substantially improved our understanding of the situation.

species in the genus found on continental Africa. *L. p. keniensis* is a subspecies occurring in the northern two-thirds of Kenya and the bordering edges of the neighboring countries. *L. somalicus* is an endemic of the arid Somali region. *L. s. battersbyi* ranges from the vicinity of the Somaliland-Ethiopian border south into northern Kenya (Fig. 1).

Turkana is a district in the extreme northwestern corner of Kenya, lying between Lake Rudolf on the east and the Uganda-Kenya border on the west. Both geographically and ecologically the area is a western outlier of the arid Somali region to the east (Schmidt, 1923; Parker, 1932, 1936, 1942).

As various parts of Turkana have been described in some detail elsewhere (von Höhnel, 1894; Worthington, 1932; Fuchs, 1935, 1939; Buxton, 1937), no more than a brief description of the area need be given here.

South Turkana, where these observations were made (Figs. 2-3), is extremely arid and consists of numerous rugged plateaus and broken hills. Between these extend vast lava and quartzite pebble sheets and barren windswept sand flats. Goats and drought have kept vegetation to a minimum except along the larger water courses, which never carry a permanent supply of water. *Acacia* is by far the most predominant plant group, and it is in the *Acacia* trees that one finds the *Lygodactylus* geckos.

The local distribution of the two species in south Turkana was a bit peculiar. Both species were quite common in the study area except along the Kerio River at Lokori (Fig. 3). This area was visited several times during the course of my two-month stay, but only three or four individuals of each species were ever seen. This scarcity was not too unusual in the case of *L. s. battersbyi* as it was always found less frequently in the large *Acacia tortilis* which is dominant along the larger water courses such as the Kerio, Kakurio, and Kalabata. *L. p. keniensis*, however, was usually very common in these acacias, except along the Kerio — an exception that merits special consideration below (see Competition section).

Food: Movement of prey organisms seems to be a prerequisite for eliciting a gecko's attention. Food items of *L. p. keniensis*, as determined by field observations and an analysis of the contents of ten stomachs, included a wide variety of invertebrates ranging in size from Diptera less than three mm long to mantids as long as the snout-vent length of the gecko itself. Most food items, however, are small (5 mm or less in length).

Perhaps the most common arthropod in the geckos' microhabitat and yet one that is never considered as food is an ant species

of the genus *Crematogaster* (species near *paolii*) — large numbers of which occur on every *Acacia*. The ants of this genus are well known for their fetid secretions (W. L. Brown and E. O. Wilson, personal communication), which may account for their being generally avoided by geckos. However, the geckos often "ambush" columns of ants returning from a raid on a tree termite nest and pluck the largest morsel from the clutches of a particularly successful raider. At other times, the ants are actively avoided, and if, on being wounded and disabled, the gecko adheres to the tree, he is soon covered with the swarming ants.

The termites of the *Acacia* always cover their paths on the surface of the tree with thin, dirt arches. When one of these arches is accidentally broken open, the workers immediately begin to repair it. During this process, a worker must expose himself to some degree for a few seconds while at the breach, and there is rarely a breach without a gecko patiently partaking of the feast. There is usually intense competition for the single position at the breach and once the dominant animal is removed, his place is quickly taken.

Both species possess great visual acuity, individuals often being attracted by a movement of a small (1-2 cm) object 2-2½ meters distant.

Both species of geckos spent a good deal of time licking the extremely viscous, amber colored exudate of the *Acacia* trees, although the reasons for such actions are unknown. Like Kästle's (1964:489) *Phelsuma,* the *Lygodactylus* geckos under my observation also licked a variety of jams and jellies, apricot being their favorite flavor.

Water economy with these geckos, as with all reptiles of the area, must be of crucial importance. No dew was ever formed during the two months of field work, and we encountered rain only twice (1, 14 August); both times the amount was insufficient to cover the ground. One day a *L. s. battersbyi* was found licking the moisture from near the mouth of a canvas water bag that was customarily hung from the tree it inhabited. The gecko appeared practically oblivious to movement around him and continued his licking for approximately 15 minutes.

Activity temperatures and periods: Cloacal temperatures of three active *L. p. keniensis* taken during the morning were 32.9, 34.5 and 35.1°C. Air temperatures at the positions from which these geckos were taken were 30.8, 32.9 and 35.5°C, respectively. Cloacal temperatures for six geckos on the initial loss of the righting reflex ranged from 43.3-44.3°C. (average 43.7°C.).

During the preliminary stages of heat distress *L. p. keniensis* behaves in a manner characteristic of many lizards, i.e., the body is raised off the ground on straightened legs, the mouth is held open, and the respiration rate increases.

Both *L. p. keniensis* and *L. s. battersbyi* are most active during the morning and late afternoon. During the mid-day they usually remain stationary, sometimes remaining in the same spot for an hour or more. I rarely saw a *Lygodactylus* on the sunny side of a branch. They usually chose to move along the underside of branches although, if this side were exposed to the sunlight, they would move along the upper, shaded side.

Approximately 15 to 30 minutes after the sun has set, foraging individuals of *L. p. keniensis* suddenly begin to ascend the branches of their trees. Some seek out a cavity in which to pass the night, but the majority of them climb to the peripheral branches and, turning so as to face the quickest avenue of escape, settle down for the night. In the morning, about 15 to 30 minutes before sunrise, they suddenly "come to life" again and quickly scurry down the branches to the main part of the tree to begin the day's foraging. *L. s. battersbyi* was also seen ascending and descending the terminal branches at approximately the same time as *L. p. keniensis*, although no individual of this species was ever observed assuming his sleeping position.

These were by far the longest activity periods of any of the diurnal lizards in the area. The lacertids and agamids rarely appeared until about an hour and a half after sunrise and retired shortly before sunset. It thus seems as if the diurnal *Lygodactylus* geckos have retained enough of their family's nocturnal heritage to enjoy the best of both worlds.

External morphology: Before proceeding with a discussion of the behavior of the two species, it will be helpful to describe briefly some of the more important aspects of color pattern and external morphology (Table 1).

Hatchling *L. p. keniensis* are 13-14 mm in snout-vent length. The dorsum is grayish brown with whitish spots which are bordered with black along their anterior edges. These whitish spots extend onto the dorsal surface of the tail where they become wider than long but are still bordered on the anterior edge by black. The result is a generally mottled and cryptic appearance. The tail is brownish orange above and orange-red below. This bright ventral color extends forward along the midventral line to the pectoral region. The dark chevron markings of the throat are faintly evident.

The change to the adult pattern entails the loss of the bright color on the tail, the change from an orange stripe to a yellow one along the ventral midline, the development of roughly longitudinal light and dark markings on the head and shoulders, and an intensification of the black on the throat.

Adult males are usually slightly larger and stockier than females. The largest male of our specimens has a snout-vent length of 35 mm; that of the largest female is 34 mm. The black on the throat of the males also tends to be slightly more extensive than in females. The light and dark chevrons and white, O-shaped postmental spot, said to be characteristic of this subspecies (Loveridge, 1947: 198, 228), are lacking in some adults of both sexes that have almost solid black throats. In the majority of the specimens, however, the "typical" pattern can be seen.

Preanal pores and escutcheon scales appear in males at a snout-vent length of about 26-27 mm. There are usually 6-8 preanal pores arranged in an anteriorly projecting, obtuse chevron. The grayish escutcheon scales are distributed in four separate areas: the underside of the thighs, directly anterior to the preanal pores and between the preanal pores and vent. Females lack these secondary sexual characters.

Both sexes have a light yellow midventral stripe on the body bordered laterally by a light gray area which extends to the dark brown dorsal color of the sides. When the animal is cold, however, the pale midventral yellow becomes a very bright mustard yellow and the dark chocolate brown color of the dorsum extends ventrad to the edge of the bright yellow stripe.

Hatchling *L. s. battersbyi* are about 11.5 mm in snout-vent length. The dorsum is a cryptic light brown with scattered white and dark brown flecks. The tail is faintly tinged with reddish orange, and the entire venter is immaculate.

Adults show little or no sexual dichromatism. Both sexes are uniformly brown above with dark brown spots on each shoulder and a few less well-defined dark brown spots on the sides. The white flecking and reddish tinge to the tail of juveniles are lacking. There is a thin dark brown horizontal stripe through the eye onto the side of the head.

Adult females average slightly larger than adult males. The largest male and female in our sample each measures 27 mm.

The smallest male with preanal pores and escutcheon scales measures 21 mm in snout-vent length. There are usually 6 preanal pores (two specimens have 5 pores) arranged in an anteriorly projecting obtuse chevron. Only the undersides of the

thighs bear escutcheon scales. Females lack these secondary sexual characters.

Both *L. p. keniensis* and *L. s. battersbyi* have black pigment in the bones of the cranium and a jet black peritoneum. These characters have been tentatively associated with diurnal habits among geckos (Kluge, 1967), although experimental work attempting to elucidate the adaptive significance of this pigment distribution has been inconclusive (Hunsaker and Johnson, 1959).

Adults and hatchlings alike of both species have the tip of the tail very slightly spatulate and provided ventrally with a double row of lamellae. In general appearance this structure closely resembles the ventral surface of the expanded digital tip. The tip of a regenerative tail has the differentiated ventral "scansorial" scales of an original tail, but it lacks the ordered arrangement of a double row.

Loveridge (1947:195), Kästle (1964:487-488), Mertens (1964), and Pasteur (1964:12,76) discuss this structure on the underside of the tip of the tail in terms of its "adhesive" or "holding" advantage for these arboreal lizards. Such a function is suggested by its gross similarity to the digital pads, the fact that resting animals often have only the extreme terminal end of the tail in contact with the substrate (see Kästle, 1964, fig. 2a) but move about with the subterminal area dragging on the substrate and the terminal area curved slightly upward, and the fact that dead animals have been seen hanging by the tail.

It is difficult to watch these two species of geckos actively foraging, especially during the late afternoon when they are most active, and not see another possible function of this terminal subcaudal expansion. During the times when an individual is very active, the tail is frequently raised in a deep arch and the tip of the tail is quickly touched to the substrate, withdrawn, and touched down again several times. In this manner the gecko quickly makes contact with parts of the surface behind him through almost 180°. In this action it seems as if the tail functions less as a grasping organ than as a tactile sensory organ. Such a tactile sensory function would, of course, be an added advantage in an arboreal life.

Display: From Kästle's (1964:494-495) description of the intraspecific display of *L. p. picturatus* it would appear that the display of *L. p. keniensis* is very similar. In "full display" an adult gecko simultaneously raises the body slightly on straightened legs, arches the back (exposing the yellow midventral stripe?), bows the neck with the snout pointing slightly down and distends the

black throat. The display may be given with the body in a head-on or broadside position relative to the individual eliciting the response. Often both body positions are assumed alternately or successively, with the displaying gecko moving closer to the antagonist in the head-on position. It is also in the head-on position that the head is sometimes quickly jerked from side to side through a small arc.

Among adults this display may be given by males to males in fighting, by males to females in courtship activities, by females to females in fighting, and by females to males in repulsing courtship overtures. Except in courtship, the displays never lasted more than a few seconds and in only two instances except for courtship did they lead to actual physical contact.

One of these cases was brought about by introducing a foreign male into a small scrub *Acacia* tree occupied by two adult females and a single male. The resident male approached the quiescent foreign male while displaying head-on and broadside until, after a close broadside display, he suddenly attacked the foreign male with such force that both geckos fell out of the tree. The resident male immediately regained his tree, but the introduced male made his way back to the tree slowly and stayed around the base for some time. Several days later, however, he was still in the same tree, but he always elicited displays from the original male whenever the two met.

The only component of the display commonly encountered separately was the distended black throat. This was often given in "mild distress" situations. Another, more common, means of aggression was a simple attack or rush at an individual. This behavior was seen in juveniles as well as adults, especially when there was a large size difference — in favor of the attacker.

During the 15 to 30 minutes after sunset that the geckos remained active, the intensity of the day's aggression between individuals declined or diminished altogether. In one instance in which two females and one male were occupying a single, small *Acacia* tree, the larger female had been chasing the smaller female and male from a favorite food supply at the base of the tree all during the afternoon. Shortly after sunset, however, and until they retired, all three adults were feeding within centimeters of each other at the site.

It is interesting to note that *L. s. battersbyi*, which is so different in color pattern from *L. p. keniensis*, displays in the same way, i.e., the body is slightly raised on straightened legs, the back arched,

the neck bowed with his head pointing downward, and the immaculate throat distended. The body may assume the head-on or broadside position alternately, and head jerking can be a part of the head-on approach.

Although both species display in the same manner and sometimes occur in the same tree, the display was never used interspecifically. Confrontations did occur, however, and they always resulted in the *L. s. battersbyi* simply being chased from the scene by a larger or more bulky *L. p. keniensis.*

The hatchlings and juveniles of both species were always completely ignored by the adults, although the adults often ate moving objects larger than the little geckos. The smaller individuals showed little fear of the adults, but they always moved aside when they found themselves in the path of an adult.

Foreign objects never elicited a display response from either species.

Courtship and mating: Courtship and mating were observed only once in *L. p. keniensis,* but the behavior was sufficiently different from Kästle's description (1964:497-498) to warrant a complete description based on my observations.

The pair was first seen about 12:35 PM on the dark vertical trunk of an *Acacia tortilis* along a large watercourse. The male was posturing in the typical display, slightly broadside to the female. She moved toward his flanks and nipped at the basal third of his tail. The male immediately completed the circle by coming around to her tail which she would then twitch back and forth across his face while moving away with him following. The courtship was interrupted several times at this point, but it was always initiated again by the female. After separating 70 to 100 cm, it appeared as if the female began searching for the male. She would approach his tail, and the male would stiffen slightly and give a few quick sideways jerks of the head. The female then nipped at his tail and he gave a full display. The female would again approach his tail, and the male, completing the circle, would come up behind her and follow closely behind as the female moved slowly away wagging her tail across his face.

Mating took place when the male continued creeping forward over the female after she had stopped, and grasped the female about the body approximately 2 mm posterior to the axilla with his forefeet. Holding the skin of the right side of the female's nape in his mouth, the male twisted his tail up and under hers from the right side, bringing their vents together with the male's tail on the female's left side. The left hind foot of the male was held on

the dorsal side of the female's left thigh at its base, and his right hind foot was on the tree trunk. After a firm union was obtained, the male dropped his forefeet from around the body of the female onto the surface of the tree. Mating lasted for about 40 minutes, after which time the female flicked her tail sideways several times and the male disengaged himself, arching his tail upward in a deep bow. Each individual proceeded to lick the area around his vent.

The cyclic turning of the female on the tail of the male and being turned upon by the male, the wagging of the tail in the face of the following male and the recurrent initiation of courtship activities by the female are elements in the courtship and mating of *L. p. keniensis* not observed by Kästle in his *L. p. picturatus*.

Males were seen to initiate courtship activity on several occasions, but were quickly repulsed by a display from the female.

Only a single mated pair of the more elusive *L. s. battersbyi* was observed. The pair was found about 10:30 AM in a shadow on the side of a scrub *Acacia*.

The male had grasped the skin of the right side of the female's nape in his jaws and had brought his vent next to hers from the left side. The male's back was slightly hunched and his tail trailed behind on the left side. The male's forefeet were employed in grasping the female around the pectoral region behind the shoulders and were not placed on the trunk. His right hind foot rested on the dorsal surface of her right thigh at its base, and his left foot was in contact with the trunk.

The female seemed to be made quite nervous by my presence. She wagged her tail from side to side, often touching the male's back. The female stayed at the same locus but frequently turned about 180°, always carrying the male with her and keeping the pair oriented along the longitudinal axis of the branch.

After breaking off copulation, the female quickly disappeared, but the male began licking his vent.

Reproduction: Both *L. p. keniensis* and *L. s. battersbyi* lay two white, hard-shelled eggs in cavities of the tree which they inhabit. Usually the termites have excavated cavities in one or more branches, and, when these are abandoned, they become favorite sites for egg deposition (Fig. 4). Eggs will be laid in a particularly favored spot year after year, the newest pair of eggs being deposited on top of the pile. In this way as many as 40 egg shells can accumulate in a single cavity.

L. s. battersbyi lays slightly smaller eggs than *L. p. keniensis* and the eggs of both species can be found in the same cavity.

Whole egg shells were frequently found with a small circular hole through the shell and the yolky contents completely removed. The most likely explanation for this loss is predation by the ants which invariably inhabit the *Acacia* trees.

Another possible predator of *Lygodactylus* eggs or young is *Homopholis fasciata,* a gecko which inhabits, almost exclusively, these same cavities in which the *Lygodactylus* species lay their eggs.

Developing eggs, hatchlings and gravid females of both species were encountered throughout July and August. The smallest females of *L. p. keniensis* and *L. s. battersbyi* with large, shelled oviducal eggs nearly ready for deposition measured 28 and 24½ mm, respectively, in snout to vent length (Table 1). In all females carrying two large oviducal eggs, the egg in the right oviduct was placed more anteriorly in the body cavity than the egg in the left oviduct.

Population structure: Almost any scrub *Acacia* over a meter in height was likely to have one or more *Lygodactylus* inhabiting it. In an attempt to get some idea of the population structure of the *L. p. keniensis* in these trees, several of them were held under observation and the adults collected as they came to light until it was felt that the entire adult complement had been collected. In one instance, a large *Acacia tortilis* was also "collected out." The results of such collecting (Table 2) showed that females outnumber males 2 to 1.

Whether the 2 to 1 sex ratio is a reflection of a disproportionate birth ratio or the result of heavy selection pressure on the males cannot be decided at present.

L. s. battersbyi is so secretive that it is impossible to satisfy oneself that the entire adult population of any one tree has been collected. The general impression, as indicated by the sex ratio of the specimens collected (18 males, 26 females), is that females may also outnumber males.

On the open expanses, where the scrub *Acacia* predominates, the population inhabiting a single tree usually consisted of a single male, one to three females and a few juveniles. This uniformity of structure is undoubtedly a reflection of the uniformity in size and form of the *Acacia* scrub. Very few scrub *Acacia* were large enough to support two or more males, although this was the rule in the much larger *A. tortilis.*

In the few instances in which more than one male inhabited a tree small enough to allow continuous observation, it was evident that males were highly territorial. Females in trees with two or more males generally restricted their foraging areas to coincide approximately with the territories of the males and were rarely seen far

outside this area. No territorial display of females was ever observed, although a female will display to another female in certain instances, such as confrontation over a food source or a cavity for egg deposition.

Confrontations over a favorite food source of limited size, such as a partially opened termite nest, indicated that dominance is largely a matter of size and not sex: a large female for instance will dominate the position at a breach in a termite archway (see above) to the exclusion of the male within whose territory the breach may be.

Kästle (1964:491) reported that his *L. picturatus* were never observed to come to the ground. Observations on *L. p. keniensis* and *L. s. battersbyi* showed that, although both species are highly arboreal, they will come to the ground when attracted by some small movement. If the tail of an individual were accidentally broken off during capture, another gecko in the tree would usually come to the ground for the thrashing tail. Geckos could also be enticed two or three feet away from the base of the tree by scattering wood termites on the ground. During the late afternoon or early evening the geckos would often stay near the ground in the base of the tree and make forays onto the ground after a small, passing invertebrate.

Individuals that were marked artificially (with paint spots) or naturally (lost tail, scars, etc.) were kept under observation for as long as three weeks, and in no case was there emigration from the "home tree." Strong arboreal tendencies and indications of territoriality make it seem likely that most individuals, once they have become established in a tree, rarely leave the tree for the rest of their lives.

Competition: As these two species obviously occupy similar niches, the ways in which competition may be reduced are of interest.

Although it was by no means unusual to find both species occupying the same tree and foraging within inches of each other, the general situation was one species to a tree. In this regard there seemed to be some correlation between the bark color of the *Acacia* inhabited and the occupant species, although no systematic analysis was undertaken to quantify this impression.

In the relatively dense stands of the dark-barked *A. tortilis* along the larger watercourses, *L. p. keniensis*, the darker species, occurred almost to the exclusion of *L. s. battersbyi*. Even in the few *A. tortilis* found along the smaller watercourses, *L. p. keniensis* greatly outnumbered *L. s. battersbyi* which might also be found in the same tree.

On the more open flats, the scrub *A. etbiaca* is the dominant tree. The bark of this species is smooth and ranges in color from light gray to dark reddish brown. In pure stands of the gray-barked trees, *L. s. battersbyi*, the lighter species, was found to the exclusion of *L. p. keniensis*.

Between these two extremes, however, the correlation became less exact and more difficult to establish. Whether this correlation, to the extent that it does exist, is due to habitat selection or random dispersal and natural selection for body color on the given substrate, or both, cannot be decided on the basis of the data at hand.

Whenever the two species were found together in the same tree, it was more frequently the case that a *L. s. battersbyi* would be found in a "*L. p. keniensis* tree" than vice versa. In such situations, the smaller *L. s. battersbyi* tended to occupy the more peripheral branches, while the larger *L. p. keniensis* would be found on the larger central trunks and branches.

Adult *L. s. battersbyi* also inhabited smaller trees and shrubs than adult *L. p. keniensis*.

Both species were often encountered separately on single trees that were quite isolated by stretches (100-200 meters) of lava or quartz pebble sheets. In one instance a male and female *L. p. keniensis* and developing eggs were found on a windswept flat in a dark-barked *Acacia* that some time previously had been stripped of its foliage leaving only the trunks and main branches (Fig. 5). During the afternoon that I worked in this area the tree was hit by three large dust devils.

Beyond these differences, however, there was little indication of any other ecological or behavioral differences between the two species. This is not too disturbing as many of these differences, which are expected on the basis of theory, are hinted at by differences in size and color patterns of the two species. For example, the size difference may be reflected by average differences in the size and kind of prey organisms taken by the two species.

It remains to explain the absence of *L. p. keniensis* from the Kerio River at Lokori (Fig. 3), while it is so common along all other large river courses investigated. It seems to me that this most peculiar local distribution may perhaps be due to the exclusion of *L. p. keniensis* by the somewhat larger *Hemidactylus brooki angulatus*. This widespread nocturnal gecko was very abundant in numerous situations along the Kerio (under the exfoliating bark of *A. tortilis* as well as in earth crevices) but was extremely rare beyond the confines of the Kerio except in the chimneys of the ubiquitous termite nests.

The Kerio has its headwaters far to the south in the high central plateau of Kenya and is undoubtedly the most nearly permanent river in this region of south Turkana. It may be that some environmental factor such as humidity is more nearly optimal for *H. b. angulatus* in south Turkana only along the Kerio and in the termite nests. Under such special conditions in an otherwise hostile environment the species may be able to occur to the exclusion of *L. p. keniensis.*

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On behalf of the whole expedition I would like to express our appreciation and thanks for the many kindnesses extended to us by Dr. and Mrs. R. J. Drysdale-Anderson and their mission staff at Lokori.

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TABLE 1

Summary of the size and color pattern differences between *Lygodactylus picturatus keniensis* and *L. somalicus battersbyi*

	picturatus	*somalicus*
Snout-vent length (in mm.) of:		
Hatchling	13-14 (N=10)	11½ (N=3)
Largest adult male	35 (N=53)	27 (N=17)
Largest adult female	34 (N=79)	27 (N=26)
Smallest male with escutcheon scales	26-27 (N=53)	21 (N=18)
Smallest female with oviducal eggs	28 (N=12)	24½ (N=3)
Color pattern of:		
Juvenile	Throat with faint dark chevrons; venter with orange-red mid-ventral stripe.	Throat and venter immaculate.
Adult	Longitudinal light and dark markings on head and shoulders; dark black throat chevrons; venter with yellow mid-ventral stripe.	Head and shoulders uniform — color of dorsum; throat and midventer immaculate.

TABLE 2

Summary of data on sex ratios of total adult complement of *Lygodactylus picturatus keniensis* inhabiting single trees

Number of adult males	*Number of adult females*	*Number of juveniles*
0	6	1 or more
1	8	1
1	3	0
1	1	0
1	3	2
1	2	1 or more
1	3	2
1	2	0
1	2	2
1	2	4 or more
1	3	2
15	21 (+4??)	several
1	2	0
0	2	1
1	1	0
1	2	4 or more
1	0	0
1	1	0
30	64	20 +

Ratio males/females = 1/2.1

Figure 2. Typical view of the open flats in the study area.

Figure 3. The dry bed of the Kerio River near Lokori.

Figure 4. Two pairs of *Lygodactylus picturatus keniensis* eggs in the termite-excavated cavity of a scrub *Acacia*. Part of the dead branch has been broken away to expose the eggs.

Figure 5. Defoliated *Acacia*, on a wind blown flat, harboring a male and female *Lygodactylus picturatus keniensis* and developing eggs.

BREVIORA

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TWO NEW SPECIES OF *AMPHITARSUS* (OPHIUROIDEA) FROM THE WESTERN NORTH ATLANTIC

Amy Schoener

INTRODUCTION

The brittlestars discussed in this paper were recently obtained from the Western North Atlantic, at depths of between 200 and 535 m. Two new species are described and both are referred to the previously monotypic genus *Amphitarsus* H. L. Clark (1941). The type species of *Amphitarsus* is *A. mirabilis* (by original designation), remarkable in possessing peculiar winglike structures on the oral surface of the disk; these structures are in reality lateral arm plates which have become greatly expanded in the genital region. The two new species have similar structures (Figs. 1, 2, 3, B). Both species are apparently rare, since only seven specimens in all have been obtained in collections which included several thousand brittlestars.

In 1941 H. L. Clark described the monotypic ophiuroid genus, *Amphitarsus,* from the Caribbean region. The familial relationship of the genus was ambiguous, since the mouth papillae, which are extremely important diagnostic characters, varied considerably, and Clark observed that "no two of the jaws look exactly alike." Clark tentatively placed it in the Amphiuridae. No further contribution towards the solution of this problem has since been made. Recent collections obtained by Drs. Robert Hessler and Howard Sanders (Woods Hole Oceanographic Institution), as part of a detailed study of benthic assemblages of the Western North Atlantic (Sanders, Hessler and Hampson, 1965), have yielded two new species of this genus, one of which apparently sheds light on its familial relationship.

Amphitarsus mirabilis Clark

Figure 1

Amphitarsus mirabilis H. L. Clark, 1941, Mem. Soc. Cubana Hist. Nat., 15 (1): 83-85, pl. 8. Holotype, MCZ 6232 from off Cayo Coco, Camaguey Province, Cuba, from 230 fathoms (420m). Two paratypes, MCZ 6398, 6399, from off Santa Clara Province, Cuba, from 175-235 fathoms (320-430m).

Description: Disk: Diameter *ca.* 6 mm. Aboral disk surface (Fig. 1, A) covered with fine granulation; very short radial areas alternate with much longer and concave interradial areas; radial shields small and narrow. Oral interradial surface (Fig. 1, B) densely covered with minute spinules or pointed granules. Oral shields rounded, pentagonal, slightly swollen, wider than long, and not granulated. Oral papillae in two groups: inner oral papillae typically two; short, swollen, and located on each side of the jaw angle, the innermost forming the pair characteristic of the Amphiuridae, but on several of the jaws two of the papillae have fused laterally into a single wide papilla; outer oral papillae consist of a group guarding the large outer oral tentacle. Genital plate appears to be fused with four basal winglike arm plates.

Arms: Reaching a length of 50-60 mm. Arm spines, 9. Ventral arm plates rather poorly defined, more or less pentagonal. Tentacle scales: 1 very large nearly round scale present throughout most of the arm; 1-3 smaller scales on basal arm joints (Fig. 1, C).

Remarks: Clark's original description was accompanied by photographs of the holotype but no detailed illustrations were included.

Amphitarsus nike[1] new species

Figure 2

Holotype: MCZ 6797, about 140 miles N. of Surinam; Latitude 7° 53.5′ N; Longitude 54° 33.3′ W. Depth: 535 m. Woods Hole Oceanographic Institution CHAIN cruise 35, Dredge Station No. 33. April 25, 1963.

Paratypes: From the same locality, MCZ 6799, 6800.

Description: Disk: Diameter of 7.4 mm measured from outer radial shield edge to opposite edge of disk. Disk subpentagonal, flattened, and covered with fine granulation. Primary and other

[1] The specific name, a nominative in apposition, refers to the Winged Victory (Nike of Samothrace).

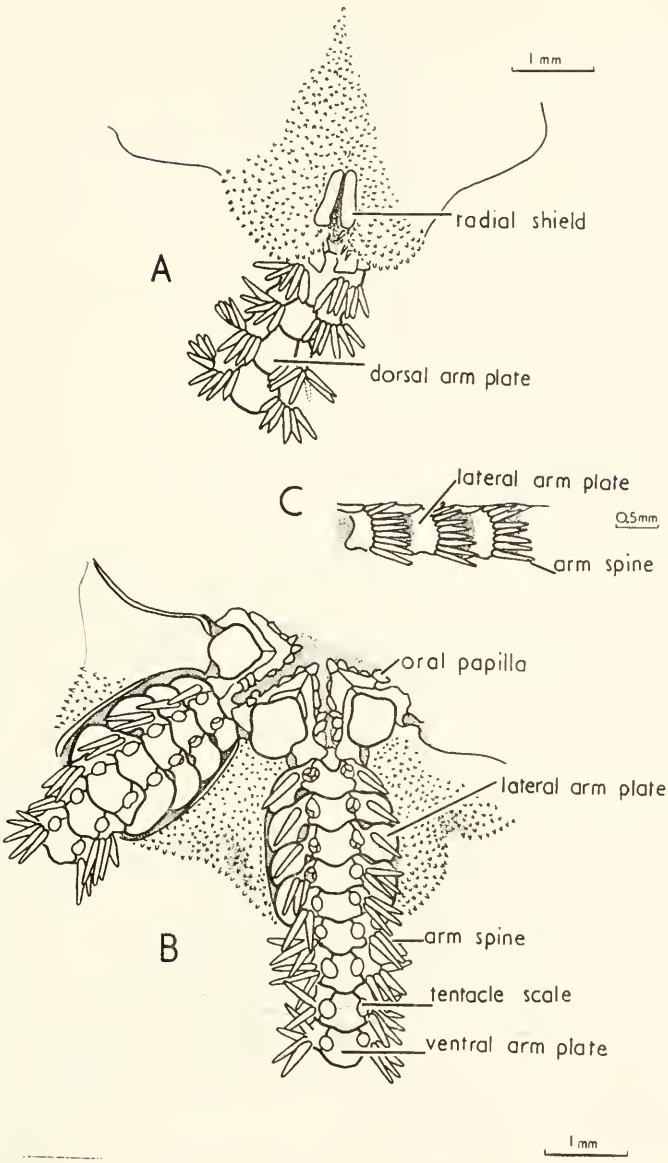

Figure 1. *Amphitarsus mirabilis* H. L. Clark, 1941. *A*, Aboral view of arm and part of disk. *B*, Oral view of two arms and part of disk. *C*, Lateral aspect of arm.

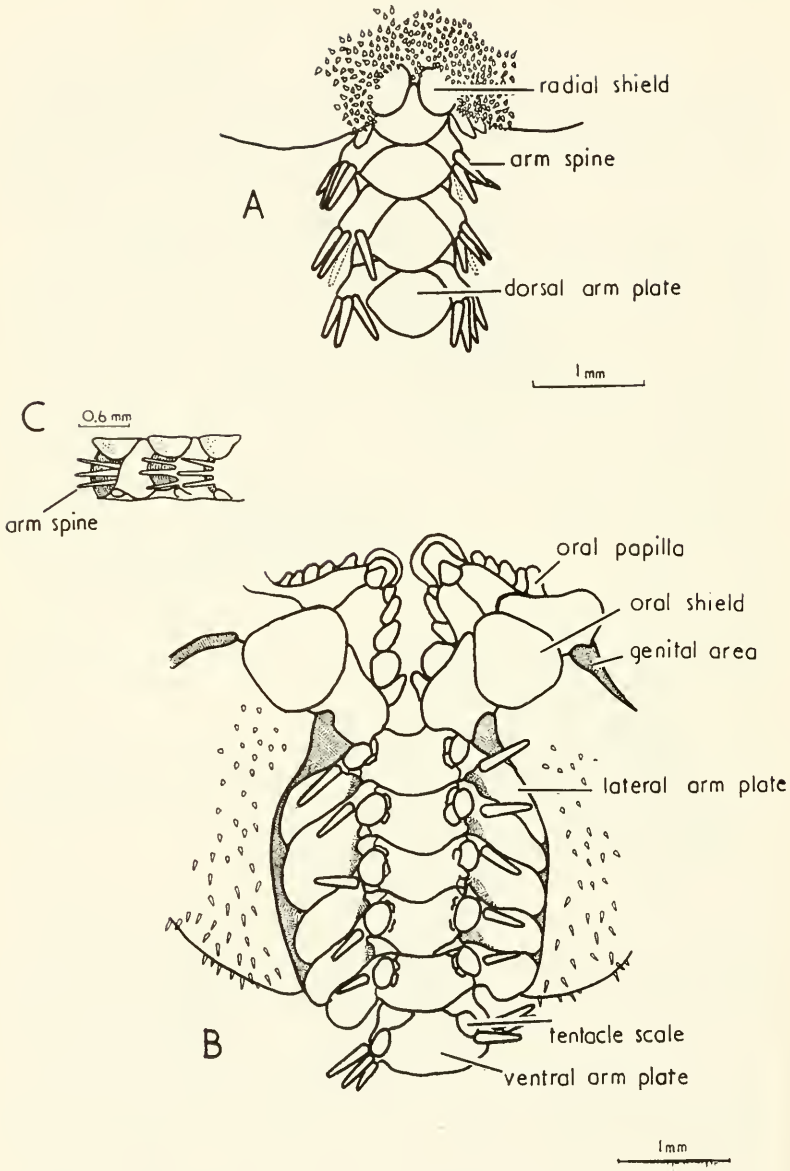

Figure 2. *Amphitarsus nike* n.sp. *A*, Aboral view of arm and part of disk. *B*, Oral view of arm and part of disk. *C*, Lateral aspect of arm.

plates not visible, and only the tips of the radial shields exposed. Midline between pairs of radial shields barely distinguishable. Oral interradial surface of disk covered with fine granulation; oral shields small, subtriangular with rounded angles and a slightly depressed convex base; length about 0.9 mm. and width 0.8 mm. Adoral shields narrow proximally, becoming much wider at base between second oral tentacle pore and oral shields. A single papilla generally present at the jaw apex, but in other cases it is difficult to distinguish whether one, two, or none of the papillae are occupying this position. Inner oral papillae: four to five, conical, becoming broader and oval towards the outer edge of the jaw. A vertical series of teeth occurs at the jaw apex. Oral tentacle pores partially visible, opening into the mouth angle. Genital clefts elongate, flaring from the ventral arm plate and narrowing at the margin of the disk; they extend from the adoral shield to the margin of the disk. These clefts are superficially partitioned by five overlapping winglike lateral arm plates; these plates begin at the second ventral arm plate and are attached to the lateral arm plate and not directly to the disk itself.

Arms: Arms incomplete, at least 36 mm beyond the disk on 7.5 mm specimen. At the arm base, the fifth (outermost) overlapping winglike lateral plate is divided into two or three flat, finger-like projections which are visible from the aboral side of the disk. Dorsal arm plates angular, broadened ovals, i.e. with obtuse angles inward in the proximal segments, becoming widely oval after the first six segments. Narrow lateral arm plates meet at the midline on both oral and aboral surfaces, thereby separating the ventral and dorsal arm plates, respectively. Arm spines: three occur on most of the lateral arm plates; four are present on those joints which carry the winglike lateral plates. Beyond the disk, upper arm spine *ca.* 0.8-1.0 arm joints in length; lower two spines increasing slightly in length, the most ventral spine being *ca.* 1.2 arm joints in length. Ventral arm plates indistinct, somewhat broadened, hexagonal, with narrower proximal portions and wider, distal, convex portions beyond the disk. Tentacle pore large, and conspicuous, round-oval; on the basal pores there are two to three tentacle scales of reduced size. Thereafter, there is a single, flat, tentacle scale covering the entire pore.

Color in life: Unknown; color in alcohol and dry specimens: whitish.

Specimens examined: Holotype and paratypes.

Amphitarsus spinifer[1] new species

Figure 3

Holotype: MCZ 6798, about 200 miles east of New York City; Latitude 40°01.8′ N; Longitude 70°42′ W. Depth: 200 m. Woods Hole Oceanographic Institution ATLANTIS cruise No. 283; WHOI Benthic Slope Station No. 2. August 28, 1962.

Paratypes: From the same locality, MCZ 6801.

Description: Disk: Disk diameter 3.8 mm from the outer edge of the radial shields to the opposite disk margin. Short radial areas alternate with longer interradial areas; disk subpentagonal, generally flat, covered with multitudinous somewhat poorly-defined scales with isolated spines present on many of them; primary plates clearly visible, much larger than the surrounding scales, irregular in shape and separated from each other by the smaller disk scales. Radial shields clearly exposed, closely paired but not touching, and less than half the disk radius in length; length about 0.6 mm and width 0.2 mm. Oral disk interradial surface covered with scales and isolated spines similar to those on the aboral surface; the spines are largest on the centro-dorsal disk surface (*ca.* 0.4 mm long), becoming slightly smaller and narrower on the disk aboral margin (*ca.* 0.3 mm long), and decreasing to 0.25 mm on the oral surface. Genital clefts elongate, flaring from the first lateral arm plate, narrowing at the disk margin, extending from the oral shield to the margin of the disk. Clefts partitioned superficially by two overlapping plates which begin at the second ventral arm plate, to whose surface these winglike lateral plates are joined. Oral shields small, length *ca.* 0.3 mm and width *ca.* 0.5 mm, rounded triangular, with a slightly convex distal margin which buds off from the triangle base thereby creating two laterally protruding bulges just proximal to it. Adoral plates long, narrow, slightly widened where they meet on the midline. Two conical oral papillae present, on each side of the jaw, the terminal one forming one side of the pair characteristic of the Amphiuridae. The second papilla is separated by a diastema and is closest to the papillae encircling the second tentacle pore. Jaw character, nearly constant in specimens examined.

Arms: In a smaller specimen (of 3.4 mm disk diameter), the arms, though broken, extend 20 mm beyond the disk edge; in the specimen described, the break is 6 mm from disk edge. At the

[1] The specific name is intended to call attention to the spiny character of the disk.

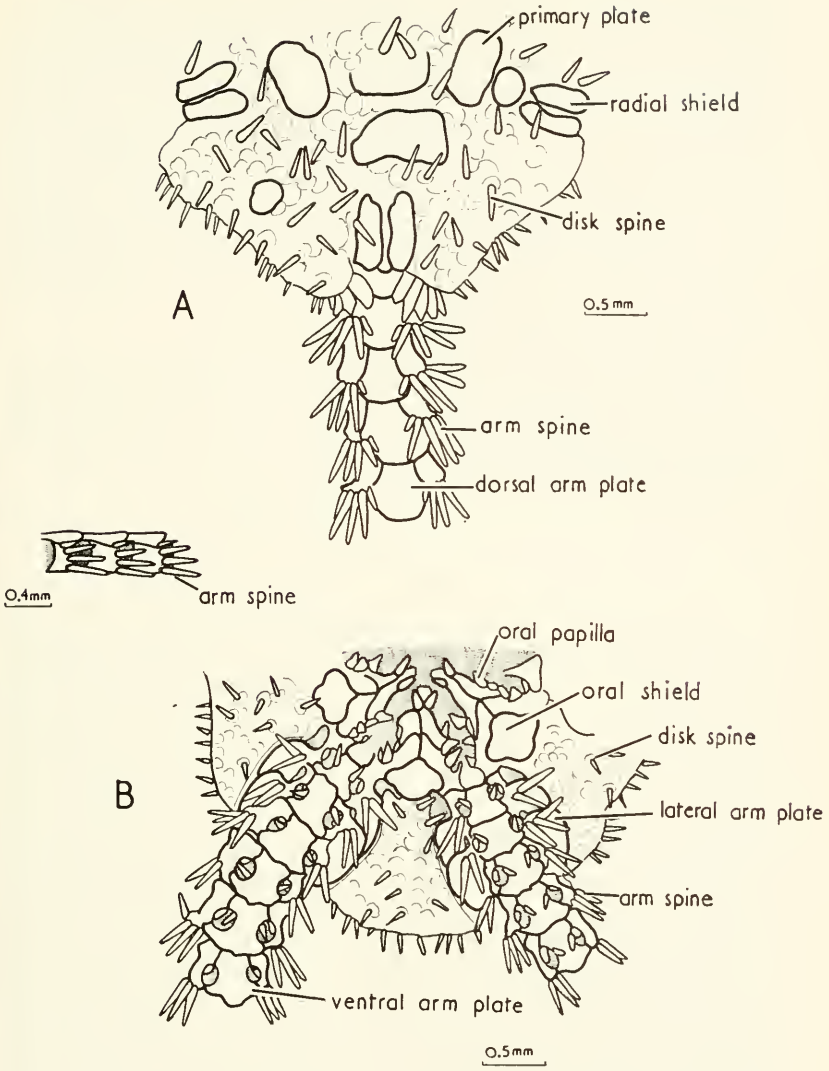

Figure 3. *Amphitarsus spinifer* n.sp. *A*, Aboral view of arm and part of disk. *B*, Oral view of two arms and part of disk. *C*, Lateral aspect of arm.

arm base, second (outermost) winglike lateral plate, visible from the aboral side, is broken into five, flattened, finger-like projections. Dorsal arm plates rounded hexagonals, length exceeding width. Arm spines: six at arm base, five to four further out on arms; two spines on joints carrying winglike lateral plates. Beyond disk, arm spines *ca.* 0.4 mm, equalling approximately the length of an arm joint; dorsalmost spine is shorter and flat. Tentacle scales: two on proximal joints; one externally placed, rounded, leaflike scale; one internally placed erect spine, attached to the median edge of the ventral arm plate (present only in first six-seven segments). Ventral arm plates basically hexagonal, with deeply emarginated lateral areas where one tentacle scale attaches.

Color in life: Unknown; color when dry: whitish.

Remarks: Three of the four paratypes were fragmented, but it was clear that they were not from the same individual, since each bore an almost complete set of primary plates on the aboral disk surface. The fourth was badly mangled.

Specimens examined: Holotype and paratypes.

DISCUSSION

The three species of the genus *Amphitarsus* illustrated and discussed above possess the singularly striking character of winglike lateral arm plates in the genital region. Although variable in number, these plates distinguish the genus from all others. If the main characteristic relating these species is taken to be these unusual winglike plates, then the genus could be placed in the family Amphiuridae, on the basis of the jaw structure of *A. spinifer*. The presence of two papillae at each jaw angle in *A. spinifer* is quite constant, even though the species is represented by smaller individuals than either of the other two species; perhaps the younger stages of *A. spinifer* differ less from the adult condition, or it may not be as immature as is suspected on the basis of size alone. The variation in the oral papillae evidenced in *A. mirabilis* and *A. nike* may be due to the immaturity of these specimens. All individuals of this genus so far as known are fairly small, although one arm fragment possibly belonging to *A. spinifer* suggests that a larger size is attained. Thus it is possible that these are young individuals, and if this is the case, they might belong to the Ophiacanthidae or even to the Ophiocomidae (Fell, personal communication).

At present the genus is known only from the Western North Atlantic. Whether or not it is truly confined to this region, only continued investigations of other areas of the ocean will tell.

This work was carried out at the Museum of Comparative Zoology during the tenure of fellowships from the International Women's Fishing Association and from Harvard University; research facilities were provided under NSF grant GB-3532, and specimens were collected by the Woods Hole Oceanographic Institution under NSF grants GB-15838 and GB-563. I wish to thank Dr. H. B. Fell of this department for his guidance and advice, Dr. R. Turner for reading the manuscript, and Drs. R. Hessler and H. Sanders for allowing me to study their collections.

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B R E V I O R A

Museum of Comparative Zoology

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ADDITIONS TO THE UNIONID FAUNA OF THE GULF DRAINAGE OF ALABAMA, GEORGIA AND FLORIDA (MOLLUSCA: BIVALVIA)

Richard I. Johnson

More than a decade has passed since Clench and Turner (1956) published their pioneering work, "Freshwater Mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River." It is not surprising that in the time since the publication of that paper certain additions and corrections have been, and can be, made concerning the Unionidae.

Athearn (1964) added two new species, *Lampsilis haddletoni* and *Villosa choctawensis*, both from the Choctawhatchee River, Alabama. Johnson (1965) described *Anodonta peggyae* which ranges from the Choctawhatchee River, Alabama, to the Hillsborough River, Florida. Athearn (1964) convincingly differentiated *Lampsilis jonesi* Vander Schalie from *L. australis* Simpson, both from the Choctawhatchee River, Alabama, and regarded as synonymous by Clench and Turner.

In 1964 Athearn collected a live specimen of *Lampsilis binominatus* Simpson in the upper Flint River drainage of Georgia, which confirmed its distinctness from *Lampsilis excavatus* (Lea) and validated the earlier records thought to be in error by Clench and Turner. An examination of the type, and of subsequently collected specimens, has clearly shown that *Alasmidonta wrightiana* (Walker) of the Ochlockonee River, Florida, is distinct from *A. triangulata* (Lea) of the Apalachicola River system of Georgia and Florida. Under *Anodontoides radiatus* (Conrad), referred to as *A. elliotti* (Lea) by Clench and Turner, are included records of *Strophitus subvexus* (Conrad) from the Chipola River, Florida. *Obovaria rotulata* (Wright) from the Escambia River, Florida, was overlooked and has recently been rediscovered.

This paper is intended to be supplemental to the work of Clench and Turner. All of the species mentioned here are figured except

Anodonta peggyae Johnson which I described and figured in 1965. *Strophitus subvexus* (Conrad), *Anodontoides radiatus* (Conrad), *Lampsilis binominatus* Simpson, and *L. jonesi* Vander Schalie are fully described. Remarks are given on *Alasmidonta wrightiana* (Walker), *Obovaria rotulata* (B. H. Wright), *Lampsilis haddletoni* Athearn, and *Villosa choctawensis* Athearn.

All of the extant types of the various named forms mentioned here have been examined and photographed. I wish to thank Mr. Herbert D. Athearn for allowing me to examine his specimen of *Lampsilis binominatus* Simpson. Thanks are also extended to Drs. K. J. Boss, W. J. Clench, and R. D. Turner for reading the manuscript and suggesting improvements.

The following abbreviations have been used.

ANSP — Academy of Natural Sciences of Philadelphia, Pennsylvania.
MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
MZUM— Museum of Zoology, University of Michigan, Ann Arbor, Michigan.
USNM — United States National Museum, Washington, District of Columbia.

All specimens mentioned in the text are in the Museum of Comparative Zoology unless otherwise noted.

Strophitus subvexus (Conrad)

Plate 1, figures 1-3

Anodonta subvexa Conrad 1834, Amer. Jour. Sci., **25**: 341, pl. 1, fig. 12 (Black Warrior River [Alabama] type, ANSP [lost]).

Margaritana connasaugaensis Lea 1858, Proc. Acad. Nat. Sci. Phila., **10**: 138 (Connasauga River, one of the headwaters of the Alabama River, Gilmer Co., Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., (2)**4**: 229, pl. 32, fig. 113; figured holotype USNM 86277. Lea 1859, Obs. Unio, **7**: 47.

Margaritana spillmanii Lea 1858, Proc. Acad. Nat. Sci. Phila., **10**: 138 ([Magbys Creek, written on type, not located on modern county map] Tombigbee River, near Columbus [Lowndes Co.] Mississippi). Lea, 1862, Jour. Acad. Nat. Sci. Phila., (2) **5**: 105, pl. 17, fig. 252; figured holotype USNM 86278. Lea, 1862, Obs. Unio, **8**: 109.

Margaritana tombecbeensis [*sic*] Lea 1858, Proc. Acad. Nat. Sci. Phila., **10**: 138 (Tombecbee River, Columbus [Lowndes Co.] Mississippi).

Margaritana tombigbeensis Lea 1862, Jour. Acad. Nat. Sci. Phila. (2) **5**: 107, pl. 18, fig. 255; figured holotype USNM 86253. Lea, 1862, Obs. Unio, **8**: 111.

Margaritana gesnerii Lea 1858, Proc. Acad. Nat. Sci. Phila., **10**: 138 (Uphaupee Creek [Macon Co.] Alabama; Chattahoochee River, below Columbia [*sic*] [Columbus, Muscogee Co.] Georgia). Lea, 1862, Jour. Acad. Nat. Sci. Phila. (2) **5**: 211, pl. 32, fig. 280; figured holotype USNM 86212 from Uphaupee Creek. Lea, 1863, Obs. Unio. **9**: 33.

Margaritana alabamensis Lea 1861, Proc. Acad. Nat. Sci. Phila., **13**: 41 (Talladega Creek [Talladega Co.] Alabama). Lea, 1862, Jour. Acad. Nat. Sci. Phila., (2) **5**: 104, pl. 16, fig. 249; figured holotype USNM 86262. Lea, 1862, Obs. Unio, **8**: 108.

Margaritana columbensis Lea 1867, Proc. Acad. Nat. Sci. Phila., **19**: 81 (Tombigbee River, near Columbus [Lowndes Co.] Mississippi, type not in USNM [lost]).

Strophitus conasaugaensis [*sic*] (Lea). Ortmann, 1923, Nautilus, **36**: 130.

Strophitus subvexus (Conrad). Frierson, 1927, Check List North American Naiades, p. 23.

Strophitus spillmanii (Lea). Vander Schalie, 1940, Lloydia, **3**: 197.

Anodontoides elliotti (Lea). *partim*. Clench and Turner, 1956, Bull. Florida State Mus., **1**: 182.

Description. Shell medium in size, reaching about 100 mm in length. Outline subrhomboidal, becoming subelliptical or trapezoidal with age. Valves inequilateral, subcompressed to rather inflated, thin. Anterior end regularly rounded, posterior end obliquely subtruncate above, rounded or subtruncate below. Ventral margin almost straight, often becoming slightly arcuate with maturity. Dorsal margin short, forming a broad angle with the obliquely descending posterior margin. Hinge ligament short but prominent. Posterior ridge generally quite broad and very faintly double. Posterior slope flat or slightly concave. Umbos moderately swollen, slightly raised above the hinge line, located from about the center to the anterior third of the valves, their sculpture consisting of a few very strong ridges running parallel to the growth lines, somewhat interrupted at the posterior ridge. Surface of the shell smooth, generally shiny, waxy yellow, greenish yellow, brownish, often rayless, though sometimes with green rays especially on the posterior slope. Occasionally the surface has numerous broad green rays which give the whole shell a greenish appearance.

Left valve with a stumpy, vestigial pseudocardinal tooth directly below the umbo, sometimes with traces of first and third teeth, before and behind it. No lateral teeth. Right valve with one rather well developed pseudocardinal, triangular and compressed, or tubercular, knob-like and stumpy.

Umbonal cavities moderately deep with dorsal muscle scars.

Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line faint. Nacre bluish, dull salmon or purplish, often spotted with yellow.

Measurements

Length mm	*Height* mm	*Width* mm	
59	36	25	Topotype of *S. subvexus* (Conrad) MCZ 146655.
62	36	24	Holotype of *M. connasaugaensis* Lea
77	52	37	Holotype of *M. tombigbeensis* Lea
92	56	39	Holotype of *M. gesnerii* Lea
93	51	40	Holotype of *M. spillmanii* Lea
116	54	38	Holotype of *M. alabamensis* Lea

Remarks. Strophitus subvexus (Conrad) of the Gulf drainage, shows some of the same diversity of shape as does *Strophitus undulatus* (Say) of the Atlantic drainage and interior basin. It is readily distinguished from *undulatus* which has entirely rudimentary pseudocardinals, represented, if at all, by slight swellings. In *S. subvexus* there is at least one pseudocardinal in each valve, and while small, they are usually well developed, triangular and compressed, or tubercular, knob-like and stumpy. It has also been confused with *Anodontoides radiatus* (Conrad), but that shell is always regularly elliptical with rays over the entire surface, while *subvexus* is subelliptical, inclined to be biangulate behind, seldom with rays over the entire surface, and with pseudocardinals that are less rudimentary.

Vander Schalie (1940) correctly reports this species from two localities on the Chipola River as *Strophitus spillmanii.* Clench and Turner (1956) assumed that Vander Schalie's specimens were *Anodontoides elliottii* (Lea) [= *radiatus* (Conrad)], but all of their records of *radiatus* from the Chipola River are *S. subvexus.*

Ortmann (1923) reviewed some of the names applied to the forms of this species, but did not include those from the Tombigbee River drainage. *S. subvexus* (Conrad), like its synonyms *connasaugaensis* Lea and *tombigbeensis* Lea, was founded on rather trapezoidal inflated individuals, while other names were given to the more common subelliptical specimens. Conrad's figured type which was about 2 inches (51 mm) in length, was specifically stated to be in the Academy of Natural Sciences of Philadelphia, but it has been lost. He did not give a precise locality, but in all

probability the type came from the Black Warrior River in the vicinity of Tuscaloosa, Tuscaloosa Co., Alabama, since Conrad is known to have been there in June of 1833 (Wheeler, 1935: 38).

Range. Gulf drainage, from the Pascagoula River system of Mississippi to the Apalachicola River system of Georgia and Florida.

SPECIMENS EXAMINED

PASCAGOULA RIVER SYSTEM

Mississippi: Edahoma Creek, 6 mi. NW Soso, Jones Co.

ALABAMA-COOSA RIVER SYSTEM

Tombigbee River Drainage. — *Mississippi:* Tombigbee River, Columbus, Lowndes Co. *Alabama:* Coalfire Creek, Coalfire, Pickens Co. Bodka Creek, 5 mi. NW Gainsville, Sumter Co. Okatuppa Creek, 4 mi. SE Toxey, Choctaw Co. Black Warrior River, Tuscaloosa Co.

Cahawba River Drainage. — *Alabama:* Black Creek, St. Clair Co. Shoal Creek, Montevallo, Shelby Co.

Coosa River Drainage. — *Georgia:* Teloga Creek; Chattooga River, Summersville; *both* Chattooga Co. *Alabama:* Mills Creek, Cherokee Co. *Tennessee:* Conasauga River, Conasauga, Polk Co. *Georgia:* Conasauga River, Gregorys Mill, 10 mi. N Eaton, Murray Co. Conasauga River, Gilmer Co. (USNM). Conasauga River, 1.4 mi. N Resaca, Gordon Co. Black Creek, St. Clair Co. Choccíocca Creek, 3 mi. S Lincoln; Talladega Creek; *both* Talladega Co.

Tallapoosa River Drainage. — *Alabama:* Uphaupee Creek, Macon Co.

Alabama River Drainage. — *Alabama:* Cub Creek, Pine Hill, Wilcox Co.

APALACHICOLA RIVER SYSTEM

Chipola River Drainage. — *Florida:* Big Creek, 8 mi. W Malone, Jackson Co. Cowarts Creek, nr. Florida state line, Houston Co. (MZUM). Reedy Creek, 6 mi. W Malone; Chipola River, 1 mi. N Marianna; *both* Jackson Co. Chipola River, Scotts Ferry, Calhoun Co. (MZUM).

Chattahoochee River Drainage. — *Georgia:* [Chattahoochee River] below Columbus, Muscogee Co. (USNM).

Flint River Drainage. — *Georgia:* Kinchafoonee Creek, 4 mi. N Bronwood, Terrell Co. Ichawaynochaway Creek, 3 mi. N Morgan, Calhoun Co.

ANODONTOIDES RADIATUS (Conrad)

Plate 2, figures 1-4

Alasmidonta radiata Conrad 1834, Amer. Jour. Sci., **25**: 341, pl. 1, fig. 10 (small streams in South Alabama; measured holotype ANSP 41147 labeled, Greene Co.)

Margaritana elliottii Lea 1858, Proc. Acad. Nat. Sci. Phila., **10**: 138 (Chattahoochee River [below Uchee Bar] near Columbus [Muscogee Co.] Georgia). Lea, 1859, Jour. Acad. Nat. Sci. Phila., (2)**4**: 226, pl. 31, fig. 108, figured holotype USNM 86257. Lea, 1859, Obs. Unio, **7**: 44.

Margaritana elliptica Lea 1859, Proc. Acad. Nat. Sci. Phila., **11**: 113 (Tombigbee River, Columbus [Lowndes Co.] Mississippi). Lea, 1862, Jour. Acad. Nat. Sci. Phila., (2)**5**: 106, pl. 18, fig. 254; figured holotype USNM 86258. Lea, 1862, Obs. Unio, **8**: 110.

Anodonta showalterii Lea 1860, Proc. Acad. Nat. Sci. Phila., **12**: 307 (Coosa River Wetumpka [Elmore Co.] Alabama). Lea, 1862, Jour. Acad. Nat. Sci. Phila., (2)**5**: 215, pl. 33, fig. 284; figured holotype USNM 86487. Lea, 1863, Obs. Unio, **9**: 37.

Strophitus radiatus (Conrad). Frierson, 1927, Check List North American Naiades, p. 23.

Anodontoides elliotti (Lea). *partim*. Clench and Turner, 1956, Bull. Florida State Mus., **1**: 182, pl. 5, fig. 3.

Description. Shell generally small to medium in size, reaching 72 mm in length. Outline elliptical. Valves inequilateral, inflated, thin. Anterior end regularly rounded, posterior end rather pointed. Ventral margin slightly curved. Dorsal margin slightly curved scarcely forming an angle with the obliquely descending posterior margin. Hinge ligament covering most of the dorsal margin. Posterior ridge generally broad and rounded, occasionally subangulate. Posterior slope flat. Umbos moderately swollen, slightly raised above the hinge line, located toward the anterior third of the shell, their sculpture consisting of a few moderate ridges that curve up sharply behind. Surface of the shell smooth, brownish or brownish green, generally with bright or dark green rays of different widths over the entire surface of the shell.

Left valve with a rudimentary, laminate, somewhat bifurcated, pseudocardinal tooth. Hinge plate very narrow. No lateral teeth. Right valve with one long, narrow, low, pseudocardinal tooth, anterior to the umbo.

Umbonal cavities rather shallow with dorsal muscle scars. Anterior adductor muscle scars clearly outlined, posterior ones obscure. Pallial line faint. Nacre bluish white, often with yellow spots toward the umbonal cavities, iridescent posteriorly.

Length mm	*Height* mm	*Width* mm	
50	29	19	Holotype of *M. elliptica* Lea
64	36	22.5	Holotype of *A. radiata* Conrad
71	35.5	25.5	Mosquito Creek, Chattahoochee, Gadsden Co., Florida.
72	43	31	Holotype of *A. showalterii* Lea

Remarks. *Anodontoides radiatus* (Conrad) of the Gulf drainage, shows the same consistency of shape as does *Anodontoides ferussacianus* (Lea) of the interior basin. It is readily distinguished from *ferussacianus* which is toothless, by the presence of a vestigial tooth in each valve. *A. radiatus* is, in general, more consistently elliptical, and has brighter, more clearly defined rays. In the Gulf drainage, *A. radiatus* has been confused with *Strophitus subvexus* (Conrad). Clench and Turner's (1956:183) records of *elliotti* [= *radiatus*] from the Chipola are all *subvexus*.

A. radiatus differs from *S. subvexus* by being a smaller species with a consistently elliptical shell, having bright green rays over the entire surface of the shell, whereas *subvexus* is subelliptical, inclined to be biangulate behind, seldom with rays over the entire surface. The hinge teeth of *radiatus* are laminate and delicate, the left valve with a single bifurcated tooth, the highest portion often being posterior to the umbo, the right valve with one long narrow tooth, parallel to the anterior dorsal margin. The hinge teeth of *subvexus* are less delicate, the left valve with a stumpy, vestigial, pseudocardinal directly below the umbo, sometimes with the trace of a first and third tooth before and behind it, the right valve with a triangular, or knob-like tooth which is not parallel to the anterior dorsal margin.

Frierson (1927:23) gives the correct synonymy of this species. Conrad's holotype of *Alasmidonta radiata* is labeled as coming from Greene Co., Alabama. In all probability the type is from a tributary of the Black Warrior River near Erie [a town, no longer extant, about 10 mi. W Greensboro, Hale Co., Alabama] since Conrad is known to have been there around the first of June 1833 (Wheeler, 1935:38).

Range. Gulf drainage, from the Alabama-Coosa River system of Alabama to the Apalachicola River system of Georgia and Florida. Absent from the intervening Choctawhatchee River system and the Chipola River of the Apalachicola River system.

SPECIMENS EXAMINED

ALABAMA COOSA RIVER SYSTEM

Tombigbee River Drainage. — *Mississippi:* Tombigbee River, Columbus, Lowndes Co. (USNM). *Alabama:* [Tributary of Black Warrior River] Greene Co. (ANSP). [Tombigbee River] Margeno Co.

Coosa River Drainage. —*Alabama:* Coosa River, Wetumpka, Elmore Co. (USNM).

Alabama River Drainage. — *Alabama:* Pine Barren Creek, Camden, Wilcox Co.

ESCAMBIA RIVER SYSTEM

Conecuh River Drainage. — *Alabama:* Oakywoods Creek, Butler Co. Dry Creek, Brantly, Crenshaw Co.

APALACHICOLA RIVER SYSTEM

Chattahoochee River Drainage. —*Georgia:* Chattahoochee River, West Point, Troup Co. (USNM). Chattahoochee River, Uchee Bar, below Columbus, Muscogee Co. (USNM). Big Uchee Creek, Young's Bridge, 6 mi. NE Seale; Big Uchee Creek, below Fort Mitchell; *both* Russell Co.

Apalachicola River Drainage. — *Florida:* Mosquito Creek, 1 mi. S. Chattahoochee, Gadsden Co.

ALASMIDONTA WRIGHTIANA (Walker)

Plate 2, figure 5

Strophitus wrightianus Walker 1901, Nautilus, **15**: 65, pl. 3 (Tributaries of the Flint River, Baker Co., Georgia; holotype MZUM 74938. Type locality corrected to Ochlockonee River, Florida, on the authority of Walker, by Simpson, 1914, Cat. Naiades, **1**: 357).

Alasmidonta triangulata (Lea). *partim*. Clench and Turner, 1956, Bull. Florida State Mus., **1**: 180.

Remarks. In the Gulf drainage, *Alasmidonta wrightiana* (Walker) has been confused with *A. triangulata* (Lea) but it differs from that species by being elliptical, rather than triangular, by having a posterior ridge that is rounded rather than sharp, and especially by having a very characteristic sculpture on the posterior slope which consists of a number of ridges that extend from the posterior ridge to the dorsal and posterior margins. *A. triangulata* is not sculptured on the posterior slope.

Long known only from the holotype, the Museum of Comparative Zoology is grateful to the Florida State Museum for a more recently collected specimen.

Range. Gulf drainage, restricted to the Ochlockonee River, Florida.

SPECIMENS EXAMINED

OCHLOCKONEE RIVER SYSTEM

Ochlockonee River Drainage. — *Florida:* Ochlockonee River, bridge, 8 mi. W Tallahassee, Leon Co.

Obovaria rotulata (B. H. Wright)

Plate 3, figure 1

Unio rotulatus B. H. Wright 1899, Nautilus, **13**: 22 (Escambia River, Escambia Co., Florida; holotype USNM 159969, figured by Simpson, 1900, Proc. Acad. Nat. Sci. Phila., p. 78, pl. 4, fig. 2).

Obovaria rotulata (Wright). Simpson, 1914, Cat. Naiades, **1**: 297.

Remarks. Obovaria rotulata (Wright) of the Escambia River, differs from *Obovaria unicolor* (Lea) of the Alabama Coosa River system by being almost circular in outline, the latter being elliptical or ovate. Overlooked by Clench and Turner, *rotulata* is the easternmost representative of *Obovaria* in the Gulf drainage. Formerly known only from the holotype, the Museum of Zoology, University of Michigan, has recently acquired specimens of this species collected by William H. Heard.

Range. Gulf drainage, restricted to the Escambia River, Florida.

SPECIMENS EXAMINED

ESCAMBIA RIVER SYSTEM

Escambia River Drainage. — *Florida:* Escambia River, Escambia Co. (USNM).

Lampsilis binominatus Simpson

Plate 2, figure 6; Plate 3, figure 2

Unio lineatus Lea 1840, Proc. Amer. Philos. Soc., **1**: 287 (Chattahoochee River, Columbus [Muscogee Co.] Georgia). Lea, 1842, Trans. Amer. Philos. Soc., **8**: 206, pl. 12, fig. 20; figured holotype USNM 84884. Lea, 1842, Obs. Unio, **3**: 44, *non Unio lineata* 'Valenciennes' Bory de St. Vincent 1827.

Lampsilis binominatus Simpson 1900, Proc. United States Natl. Mus., **22**: 528, new name for *Unio lineatus* Lea 1840.

Lampsilis excavatus (Lea). *partim.* Clench and Turner, 1956, Bull. Florida State Mus., **1**: 198.

Description. Shell rather small in size, not reaching over 58 mm in length. Outline of male elliptical; of female obovate. Valves inequilateral, somewhat inflated, and rather thin. Anterior end regularly rounded, posterior end distinctly pointed in the male, somewhat truncated in the female. Ventral margin straight or slightly curved in males, often extending below the base line in females. Dorsal margin short and straight, forming a broad angle with the obliquely descending posterior margin. Hinge ligament short but prominent. Posterior ridge faintly double, rather rounded and poorly defined. Posterior slope slightly concave, usually with a few faint ridges and wrinkles. Umbos moderately swollen, slightly raised above the hinge line, located toward the anterior third of the shell, their sculpture not observed. Surface of the shell smooth and shiny, waxy yellow, greenish yellow, sometimes brownish, with very fine, slightly interrupted, dark green rays over the entire surface of the shell.

Left valve with two serrated pseudocardinals, one in front of the other, the anterior one somewhat triangular, the hinder one much lower. Hinge line short but with a considerable interdentum, before two short straight lateral teeth. Right valve with two pseudocardinals, separated by a deep pit, the anterior tooth vestigial, the hinder one rather chunky and triangular; one lateral tooth.

Umbonal cavities rather deep with dorsal muscle scars. Anterior adductor muscle scars well impressed, posterior ones less so. Pallial line faint. Nacre bluish white, or salmon colored

Measurements

Length mm	*Height* mm	*Width* mm	
33	23	16	Holotype of *U. lineatus* Lea, female
37	28	19	Chattahoochee River, Columbus, Muscogee Co., Georgia, female
38	25	18	*Ibid.*, male
58	41	32	Line Creek, ½ mi. W Digbey, Spaulding Co., Georgia, male

Remarks. Lampsilis binominatus Simpson of the upper Flint River drainage, has been confused with *Lampsilis excavatus* (Lea) which ranges from the Amite River in Louisiana to the Escambia River of Alabama and Florida. *L. binominatus* appears to be a much smaller species. When specimens of the same size of both

species are compared, the males of *binominatus* are more elliptical, and specimens of both sexes have narrower, sharper, darker green rays which are consistently linear and do not broaden and become diffuse as do the rays of *L. excavatus*.

Clench and Turner did not find *L. excavatus* east of the Escambia River, and since they did not recognize *L. binominatus*, they assumed its type-locality to have been in error. Subsequent collecting has substantiated the original locality.

Range. Gulf drainage, limited to the Upper Apalachicola River system.

SPECIMENS EXAMINED

APALACHICOLA RIVER SYSTEM

Chattahoochee River Drainage. — *Georgia:* Chattahoochee River, Westpoint, Troup Co. (H. D. Athearn, formerly Boston Soc. Nat. Hist. 3526). Chattahoochee River, Columbus, Muscogee Co.

Flint River Drainage. — *Georgia:* Line Creek, ½ mi. W Digbey, Spaulding Co. (H. D. Athearn).

Lampsilis jonesi Vander Schalie

Plate 3, figure 5

Lampsilis jonesi Vander Schalie 1934, Nautilus, **47**: 125, pl. 15, figs. 1a, 1b, 2, 3a, 3b (Pea River, Priston's Mill, Dale Co., Alabama; holotype, Alabama Mus. Nat. Hist.)

Lampsilis australis Simpson, *partim*. Clench and Turner, 1956, Bull. Florida State Mus., **1**: 182.

Lampsilis jonesi Vander Schalie. Athearn, 1964, Nautilus, **77**: 138.

Description. Shell generally small to medium in size, reaching 48 mm in length. Outline subovate or elliptical, moderately elongate. Valves inequilateral, not much inflated, and rather solid. Anterior end regularly rounded, posterior end generally distinctly biangulate. Ventral margin slightly curved. Dorsal margin slightly curved, forming a sharp angle with the obliquely descending, doubly scalloped, posterior margin. Female shells show general swelling of the disc below the posterior ridge, and the ventral margin is more angular than that of the male shell. Hinge ligament short. Posterior ridge broad, but distinctly double. Posterior slope slightly concave. Umbos moderately swollen, slightly raised above the hinge line, located toward the anterior quarter of the shell, their sculpture not seen. Surface of the shell smooth, shining,

olivaceous green or olivaceous yellow, usually with irregularly distributed green rays.

Left valve with two solid, compressed, jagged pseudocardinals, a slight interdentum, and two thin slightly granular lateral teeth. Right valve with two pseudocardinals, the more posterior one rudimentary, the anterior one well developed, stumpy, and jagged; one lateral tooth.

Umbonal cavities shallow, with traces of dorsal muscle scars. Anterior muscle scars well impressed, posterior ones less so. Pallial line distinct anteriorly. Nacre bluish-white, thickened anteriorly; thinner and slightly iridescent posteriorly.

Measurements

Length mm	*Height* mm	*Width* mm	
46	22.5	16	Lectotype of *L. jonesi* Vander Schalie
48.5	23	18	Allotype

Remarks. Lampsilis jonesi Vander Schalie of the Choctawhatchee River system has been confused with *Lampsilis australis* Simpson, a species which occurs in the Choctawhatchee and Escambia drainage systems. The posterior ridge of *L. jonesi* is double, often with a distinct tertiary ridge above. The extremities of the ridges form a scalloped edge posteriorly, a unique character. The posterior ridge of *australis* is poorly defined and ends in a blunt point. The periostracum of *jonesi* is somewhat coarse, while that of *australis* is often smooth and glossy. *L. jonesi* is somewhat cylindrically shaped, *australis* is more elliptical and less inflated. Females of *jonesi* exhibit a swelling of the disc below the posterior ridge, rendering the ventral margin slightly angular, while those of *australis* only show a greater rounding of the ventral margin.

Vander Schalie compared *jonesi* to *Lampsilis subangulata* (Lea) which he said occurred with it in the Choctawhatchee River system, but these were actually specimens of *australis* since *subangulata* is restricted to the Apalachicola and Ochlockonee River systems. The two records of Clench and Turner (1956:198) from the Choctawhatchee River system listed as *subangulata* are *australis*.

Lampsilis subangulata and *australis* are allopatric. *Lampsilis subangulata* is generally more attentuate and pointed posteriorly, more inflated, with a sharper posterior ridge and a more excavated posterior slope. The surface is more highly polished and the green rays are sharper and brighter.

Vander Schalie did not specifically designate a holotype for *L. jonesi* though he makes it clear that it is in the Alabama Museum

of Natural History. It is assumed that he intended the male specimen shown on his plate 15, figures 1a, 1b, to be the holotype. It is here selected as the lectotype.

Range. Gulf drainage, restricted to the Choctawhatchee River system of Alabama and Florida.

SPECIMENS EXAMINED

CHOCTAWHATCHEE RIVER SYSTEM

Pea River Drainage. — *Alabama:* Pea River, Elamville, Barbour Co. Pea River, Priston's Mill, Dale Co. Pea River, Flemings Mill, Coffee Co.

Choctawhatchee River Drainage. — *Alabama:* East Fork Choctawhatchee River, Midland City, Dale Co. East Fork Choctawhatchee River, 8 mi. W Abbeville, Henry Co. West Fork Choctawhatchee River, 7 mi. SE Ozark; Choctawhatchee River, 1 mi. N Newton; *both* Dale Co.

LAMPSILIS HADDLETONI Athearn

Plate 3, figure 3

Lampsilis haddletoni Athearn 1964, Nautilus, **77**: 135, pl. 9, figs. g, h. (Choctawhatchee River, West Fork, 7 mi. SW Ozark, Dale Co., Alabama; holotype, National Museum of Canada 20095).

Remarks. Lampsilis haddletoni Athearn is known only from the two specimens collected at the type locality. It "appears somewhat similar to *L. ochracea* (Say) [of the Atlantic drainage]. It is smaller than that species, less inflated, the shell thicker, and the cardinal teeth are much larger. The species differs from *Villosa choctawensis* Athearn by its orbicular outline, flesh colored nacre and in particular in the coloration of the epidermis [periostracum]. The [periostracum] of *L. haddletoni* is darker anteriorly on the disc while it is lighter near the ventral margin and on the posterior slope. Rays are prominent only on the posterior slope. The [periostracum] of adult *V. choctawensis* is dark throughout except in the vicinity of the umbones where it appears lighter and exhibits fine rays." (Athearn)

VILLOSA CHOCTAWENSIS Athearn

Plate 3, figure 4

Villosa choctawensis Athearn 1964, Nautilus, **77**: 137, pl. 9, figs. c, d, e, f. (Choctawhatchee River, 2 mi. SW Caryville; about 1 mi. downstream from U. S. Highway 90, Holmes Co., Florida; holotype National Museum of Canada 20096).

Pleurobema strodeanum (B. H. Wright). *partim.* Clench and Turner, 1956, Bull. Florida State Mus., **1**: 161.

Remarks. "*Villosa choctawensis* has probably been mistaken for *Pleurobema strodeanum* B. H. Wright by collectors in the past. The males of *V. choctawensis* are strikingly similar to that species. However, they lack the consistently well defined posterior ridge of *P. strodeanum.* The male and female shells of *P. strodeanum* are essentially alike as is characteristic of shells of the genus *Pleurobema.* Sexual dimorphism is well defined in specimens of *V. choctawensis.*

"The nacre of the posterior area of *V. choctawensis* lacks most of the bluish appearance found in that area of *P. strodeanum. V. choctawensis* is in some respects similar to *V. villosa* B. H. Wright but is much shorter than that species." (Athearn) The records below are supplemental to those given by Athearn.

Range. Gulf drainage, restricted to the Choctawhatchee River system.

SPECIMENS EXAMINED

CHOCTAWHATCHEE RIVER SYSTEM

Pea River Drainage.—*Alabama:* Pea River, ½ mi. SW Geneva, Geneva Co.

Choctawhatchee River Drainage.—*Florida:* Choctawhatchee River, 8 mi. W Miller's Cross Roads, Holmes Co.

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PLATE 1

FIG. 1, *Strophitus subvexus* (Conrad). Black Warrior River, Tuscaloosa Co., Alabama. Topotype MCZ 146655. Length 59, height 36, width 25 mm (nat. size).

FIG. 2, *Strophitus subvexus* (Conrad). [Magbys Creek of] Tombigbee River, near Columbus [Lowndes Co.] Mississippi. Holotype USNM 86278 of *Margaritana spillmanii* Lea. Length 93, height 51, width 40 mm (slightly reduced).

FIG. 3, *Strophitus subvexus* (Conrad). Cowarts Creek, nr. Florida state line, Houston Co., Florida. MZUM 138467. Length 86, height 47, width 37 mm (slightly reduced).

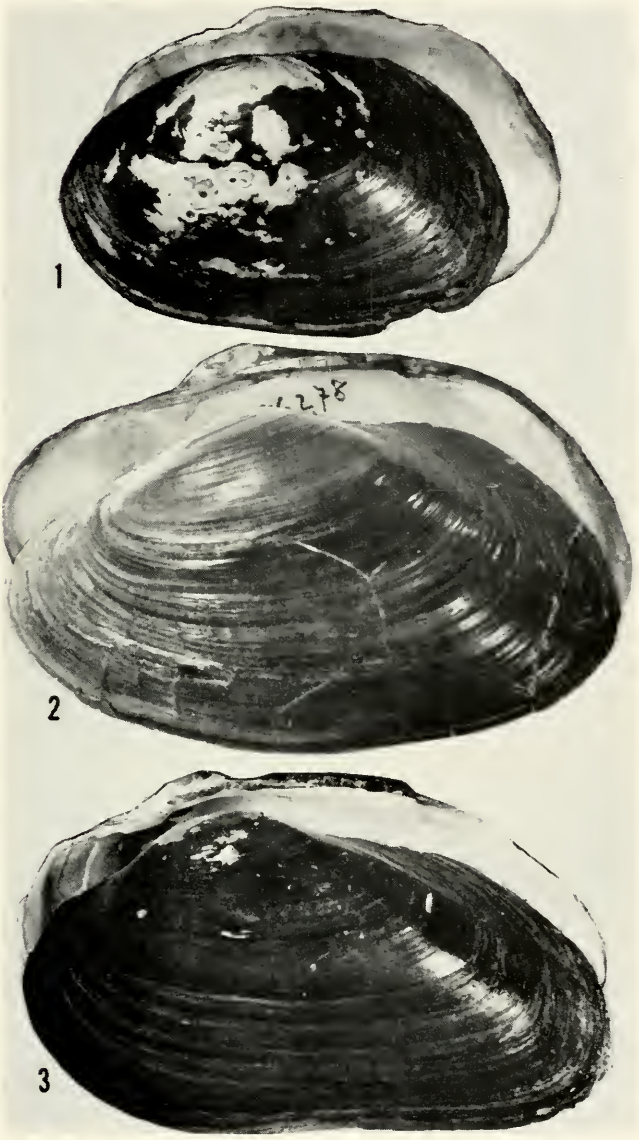
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PLATE 2

FIG. 1, *Anodontoides radiatus* (Conrad). [Tributary of Black Warrior River, Greene Co., Alabama]. Holotype ANSP 41147. Length 64, height 36, width 22.5 mm (slightly reduced).

FIG. 2, *Anodontoides radiatus* (Conrad). Chattahoochee River [below Uchee Bar] near Columbus [Muscogee Co.] Georgia. Holotype USNM 86257 of *Margaritana elliottii* Lea. Length 45, height 26, width 18 mm (slightly reduced).

FIG. 3, *Anodontoides radiatus* (Conrad). Tombigbee River, Columbus [Lowndes Co.] Mississippi. Holotype USNM 86258 of *Margaritana elliptica* Lea. Length 50, height 29, width 19 mm (slightly reduced).

FIG. 4, *Anodontoides radiatus* (Conrad). Coosa River, Wetumpka [Elmore Co.] Alabama. Holotype USNM 86487 of *Anodonta showalterii* Lea. Length 72, height 43, width 31 mm (slightly reduced).

FIG. 5, *Alasmidonta wrightiana* (Walker). Ochlockonee River, Florida. Holotype MZUM 74938. Length 54, height 38, width 31.5 mm (nat. size).

FIG. 6, *Lampsilis binominatus* Simpson. Chattahoochee River, Columbus [Muscogee Co.] Georgia. Holotype USNM 84884 of *Unio lineatus* Lea. Length 33, height 33, width 16 mm, female (slightly reduced).

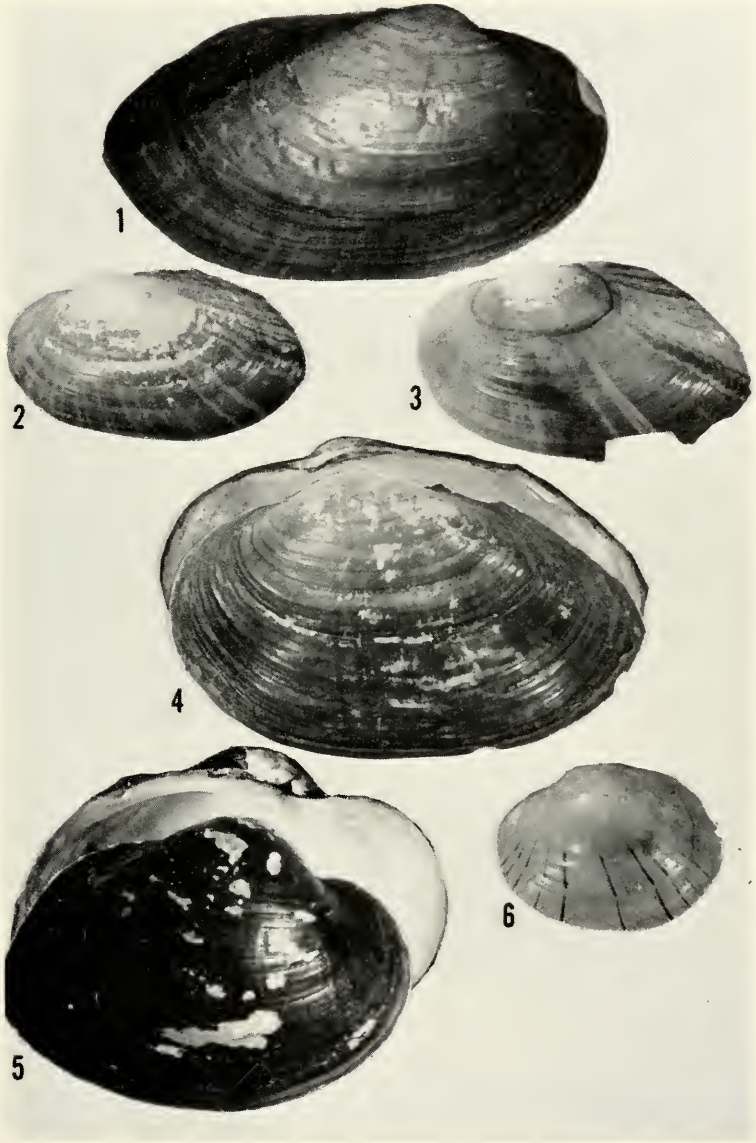
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PLATE 3

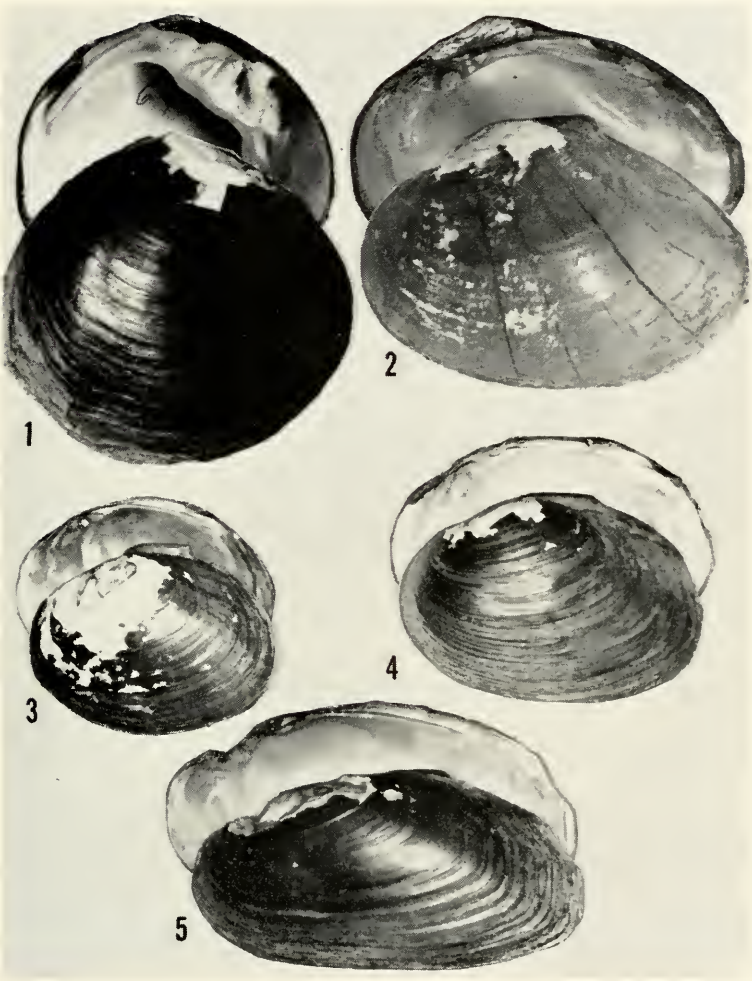
FIG. 1, *Obovaria rotulata* (B. H. Wright). Escambia River, Escambia Co., Florida. Holotype USNM 159969. Length 48, height 45, width 32 mm (nat. size).

FIG. 2, *Lampsilis binominatus* Simpson. Line Creek, ½ mi. W. Digbey, Spaulding Co., Georgia. Collection of H. D. Athearn. Length 58, height 41, width 32 mm, male (slightly reduced).

FIG. 3, *Lampsilis haddletoni* Athearn. Choctawhatchee River, West Fork, 7 mi. SW Ozark, Dale Co., Alabama. Holotype National Museum of Canada 20095. Length 30, height 23, width 12.5 mm (slightly enlarged).

FIG. 4. *Villosa choctawensis* Athearn. Choctawhatchee River, 2 mi. SW Caryville; about 1 mi. downstream from U. S. Highway 90, Holmes Co., Florida. Holotype National Museum of Canada 20096. Length 37, height 26, width 16.5 mm, male (slightly enlarged).

FIG. 5, *Lampsilis jonesi* Vander Schalie. Pea River, near Elamville, Barbour Co., Alabama. While not exactly from the type locality, this specimen was received from Vander Schalie labeled as a paratype, MCZ 98802. Length 48, height 24, width 16 mm, female (slightly enlarged).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BREVIORA

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CHELONIA DEPRESSA GARMAN RE-INVESTIGATED

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Alice G. C. Grandison,[1]
and Archie F. Carr, Jr.[2]

The pantropical sea turtle genus *Chelonia* is characterized by the tendency to mass at restricted breeding places — islands or bits of shore — where copulation as well as nesting takes place. Desultory nesting by females going separately ashore occurs in intervening regions, but by far the greater part of the reproduction of the genus takes place in aggregations. Results of extensive recent tagging studies have revealed that members of a nesting assemblage may converge from several different year-around feeding grounds, some of which may lie as far as a thousand miles away. This site tenacity in breeding is so strong that one wonders how new nesting colonies are ever established. The genus may therefore be strongly fragmented genetically, and nascent species, or even quite genuine species, may currently be confused under the collective name *Chelonia mydas*. The surprising thing is that this isolation has produced so little well-marked morphologic divergence. One example of the degree of differentiation that occurs is shown by Carr and Hirth (1962), but material representing the numerous isolated breeding populations of the genus is still too meagre to support an extensive revision of the group. One local population, however, is morphologically so distinct that it may be tentatively regarded as a species, even though only about 40 specimens are at present known to have been preserved in museums. This sharply distinguished taxon is *Chelonia depressa* Garman, described in 1880.

The type of *C. depressa* is a mounted adult male in the Museum of Comparative Zoology (MCZ 4473), with the locality "North Australia." It is a flat-shelled turtle with short flippers, and with

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[2] Department of Zoology, University of Florida, Gainesville, Florida.

only three postoculars on either side. The squamation of both fore and hind limbs is notably weak. In superficial appearance this could be equally well a freakish specimen of *Chelonia mydas* or some sort of *Lepidochelys*.

The type is still one of the few adults known. However, our own examination of the type and of hatchlings and young turtles from the vicinity of the type locality and data generously provided for specimens in Australian museums (see Table 1) leave little doubt that there exists a distinct north and northeast Australian population of *Chelonia*, clearly differentiated from other known forms of the genus, for which the name *depressa* is available.

Boulenger in 1889 placed *C. depressa* in the synonymy of *C. mydas*, although he had one juvenile specimen of the Garman species at hand, in the British Museum collections. A year later, believing that Boulenger was in error, Baur proposed elevating *depressa* to generic rank on the basis of trivial features of the lower jaw seen in the type. Baur's opinion was generally ignored, and *C. mydas* and *C. depressa* have almost universally continued to be regarded as conspecific. Probably the principal reason for the rejection of Garman's species by the majority of herpetologists has been the absence from most institutions of any material of the form. Even the careful re-appraisal of the characters of *depressa* by D. B. Fry in 1913, on the basis of seven specimens from northern Australia and adjacent New Guinea waters, did not carry the day. The issue may have been somewhat clouded by McCulloch's (1908) attempt to erect a new genus and species (*Natator tessellatus*) for a specimen which Fry was able to show was clearly identical with *depressa*. However, it was also unfortunate that Fry, after providing a superlative case for the distinctness of *depressa* on the basis of external characters, went on to place emphasis on certain skull characters (he had only one subadult skull of *depressa*) which are subject to considerable individual variation. Skepticism was only reinforced when Barbour (1914) revealed that Garman's own original series was composite and that the young specimen (MCZ 1413) was a typical *mydas* according to Fry's newly provided characters.

The down-grading of Fry's study — much more than the neglect of Garman's inadequate description — was truly unfortunate. More than 50 years later we can add no new really useful characters to those offered by Fry. Most of Fry's characters are indeed subject to some individual variation and others are difficult to state objectively, but in aggregate they — at least those based on externals — build a clear diagnosis of *depressa* and suggest that

it may be the most trenchantly differentiated local population of any of the five sea turtle genera anywhere in the world.

We have checked 15 characters in the material examined. We list these characters below, with the condition characteristic of *depressa* in parenthesis in each case.

1. Shape of the carapace (oval in *depressa*).
2. Contact of first vertebral and first marginal (rarely present in *depressa*).
3. Postanal plastral scutes (frequent in *depressa*).
4. Brachial plates (often absent in *depressa*).
5. Shields between first inframarginals and humeral (one only in *depressa*).
6. Relative length of pastral plates (femoral longest in *depressa*).
7. Size of forelimb (short in *depressa*).
8. Scales of forelimb (wrinkled skin overlying phalanges in *depressa*).
9. Scales of hind limb (wrinkled skin overlying phalanges in *depressa*).
10. Number of postoculars (3 in *depressa*).
11. Prefrontal length relative to supraocular (equal or less in *depressa*).
12. Contact of prefrontal and maxillary sheath (no or very limited contact in *depressa*).
13. Number of postparietals (1 or 3 in *depressa*, not symmetrically divided).
14. Upper eyelid scales (scales uniformly small in *depressa*).
15. Number of scales posterior to postoculars (subtemporals) (numerous in *depressa*).

Each of these characters is of some use for the recognition of *depressa* but most are *not* key characters. It is clear from the statement of some of them that there is individual variability (e.g. marginal vertebral contact, postanals). Others, such as the shape of the carapace or the size of the forelimbs, are relatively difficult to make objective since allometry will modify the condition at various sizes. Still others (e.g. upper eyelid scales) are obvious when comparative material is available but in the absence of readily repeatable counts are sometimes equivocal.

Two characters *in combination*, however, do appear absolutely and unequivocally to define *depressa* as against other Green Turtles anywhere. These are the postocular scale count of 3, *plus* the areas of wrinkled skin distally on fore and hind limbs. In

reality, the last character may be sufficient, since we know of no overlap or approach in this feature at all.

There is, unhappily, rare overlap in the postocular count, although this also is usually diagnostic. All known *depressa* have 3 postoculars. In all other populations sampled by us and in material available in the British Museum, the Museum of Comparative Zoology, the United States National Museum, and the American Museum of Natural History a count of 3 postoculars on each side, without evidence of aberrant fusion with other scales, is very rare indeed, almost inconsequential (but see below). The extreme infrequency of 3 postoculars in non-*depressa* populations is shown with great clarity in Table 2, in which counts from 3,000 specimens from one East Pacific and two Atlantic localities are given; at least one other aberrant count in the table is a more frequent variation than the 3-3 count. Only one British Museum specimen, one from the Great Barrier Reef, is equivocal in these two crucial characters. It has postocular counts of 3-4 and counts across the forelimb of 6-7. It seems, however, on most characters to be *mydas*, and the three other members of the small series collected at the same time are unquestionable *mydas*, though one other has a 3-3 postocular count. (One Museum of Comparative Zoology specimen [MCZ 9471] from Murray Id., Torres Strait, likewise has a 3-3 postocular count.)

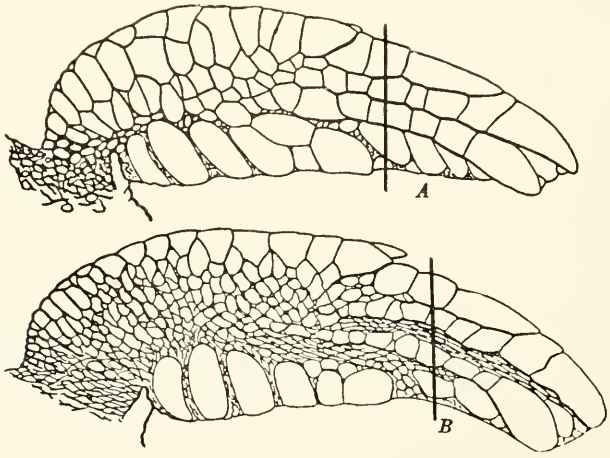

Figure 1. Forelimbs of *Chelonia mydas* (A) and *Chelonia depressa* (B) compared to show suggested places for counting scales across limb. (Modified from Fry, 1913.)

The disturbing element here is not the occasional overlap in characters but that the overlap occurs in the relatively small sample we have from the known range of *depressa*. The dearth of information on the distribution of breeding grounds of *Chelonia* in Australia makes it difficult to judge whether, and to what degree, *depressa* and *mydas* may nest sympatrically. There is an important nesting colony of *mydas*-like turtles on Capricorn Reef at the southern end of the Great Barrier Reef — especially on Heron Island and Northwest Island, at 23°30′S (Moorhouse, 1933). The islands of Torres Strait are, or used to be, heavily used for nesting by one or more forms of *Chelonia*, and Stokes (1846) reported abundant nesting both in the Gulf of Carpentaria and at Baron Island on the western Australian coast, at 20°45′S, 115°30′ W. In none of these cases is it known whether the turtle involved is *mydas* or *depressa*.[1]

The presence of the areas of wrinkled skin on the flippers of *depressa* is an even better method of diagnosing *depressa* than the three postoculars. The condition can clearly be shown in a comparative figure (such as Fry, 1913, fig. 46 a and b, and our photographs). However, a simple count will solve the problems of those who may feel, in the absence of actual comparative material, that they have an ambiguous or intermediate condition in front of them. A count of scales across the dorsal surface of the forelimb, two scales distal to the claw, will in *Chelonia mydas*

[1] Harold Cogger (Australian Museum) writes in a letter of March 9, 1967, "I'm afraid that I can give you little information re breeding sites of this species or of *C. mydas* along the north coast of Australia. *C. depressa* certainly breeds in many areas, and at the moment David Lindner, who collected our adult, currently has several *depressa* nests under observation at Port Essington. Despite frequent reports of *mydas* breeding in the area, we have no authentic records. As you know we have no specimens of *mydas* sympatric with our dozen or so specimens of *depressa*. I have written to David Lindner asking him to obtain all possible information on the occurrence of *mydas* in the area."

For the northeast coast of Australia — the other portion of the known range of *C. depressa* — J. T. Woods, Director of the Queensland Museum, reports sympatry between *C. mydas* and *C. depressa* over a stretch between Townsville and Heron Island (the latter approximately opposite Keppel Bay) but no overlapping records further north. Data that Mr. Woods has generously provided indicate that the eastern Queensland specimens of *C. mydas* adjacent to *C. depressa* localities are quite typical. However, since breeding range and residence range are for these turtles usually quite distinct, further information is much to be desired.

almost always be 4 or 5, while in *Chelonia depressa* the same count (*including always the small weak scales between the larger ones*) will be 7 to 10.

Most of the characters of *depressa* involve what appears to be a general weakening or reduction of the scalation. Besides the fewer postoculars, the lateral temporals and brachials are reduced in number, and the scales of the eyelid and forelimb are reduced in size. Series of specimens of *depressa* of several size groups will be required for final evaluation of certain of the other differentiating characters; for example, the broader and shorter fore flipper, the greater width of the head and the special texture of the areolar areas in the laminae of the hatchling.

A survey of the breeding and feeding range of *depressa* will reveal aspects of its ecology that will surely help clarify the status and relationships of the population. The short foreleg and broad skull, for example, if fully verified, may prove to be features of a carnivorous forager, like *Caretta* and *Lepidochelys* which poke about rocky places preying on crabs and mollusks, and hence do not make regular journeys between underwater pastures of turtle grass or algae and sleeping places and nesting beaches as typical populations of *Chelonia* do. That *depressa* may be a carnivorous *Chelonia* is also suggested by Fry's citing (1913:165) of the opinion of Hugh Christie that its meat is disagreeable in taste. However, it should be noted that Christie insisted that, "*C. depressa* is purely a vegetarian as far as my observations go. . . ." As Fry stated (1913, footnote, p. 165), the disagreeable taste may well have kept *depressa* out of turtle markets and thus out of the sight of zoologists. Green turtles with inferior eating qualities turn up in other places too, and these seem consistently to have a tendency to feed on invertebrates instead of plants. While the dietary divergence is, in other populations, not correlated with strong morphological differentiation, this may simply mean that *depressa*, with its putatively peculiar feeding regimen, has been isolated for a longer period of time than they. Studies of the feeding habitats and habits of *depressa* as well as of its sexual cycle and nesting ethology are needed; this work when done will greatly augment our understanding of a long neglected species.

ACKNOWLEDGMENTS

For the opportunity to examine material or for critical information on specimens not borrowed, we are indebted to L. D.

Brongersma (Leiden Museum), R. Inger (Field Museum, Chicago), H. Cogger (Australian Museum, Sydney), J. L. Woods (Queensland Museum), W. D. L. Ride, G. M. Storr (Western Australian Museum), M. Tyler (South Australian Museum). Data on Atlantic and Caribbean *Chelonia* were obtained with the support of the National Science Foundation, the Office of Naval Research, and the Caribbean Conservation Corporation.

TABLE 1

The known specimens of *Chelonia depressa*[1]

*1.	Type, MCZ 4473, "North Australia" — adult
*2.	BM 87-5.16.3, "N. W. Australia" — juvenile
*3.	FMNH 97086, Green Island near Cairns, Great Barrier Reef, Queensland, Australia — juvenile
*4.	MCZ 54713 = J 1111, Queensland Mus., no data — juvenile — not seen by Fry but the fourth Queensland Museum specimen cited by him
*5.	MCZ 54714 = J 3065, Queensland Mus., Cape Bowling Green, mid-East Queensland — juvenile
*6.	Type, *Natator tessellatus* — Port Darwin, Australian Mus. — Northern Territory, Australia = Fry specimen No. 6 — juvenile
*7.	Australian Mus. — Port Darwin, Northern Territory, Australia = Fry specimen No. 1 — juvenile
*8.	Australian Mus. — Torres Strait = Fry specimen No. 4 — juvenile
9.	Australian Mus. — Murray Island = Fry specimen No. 7, Torres Strait (skull removed, figured by Fry) — half grown
10-11-12.	Queensland Mus., J 184, J 185 (2), no data — not "New Guinea?" as stated by Fry = Fry specimens Nos. 2, 3, 5 — destroyed since Fry's time because of poor condition — juveniles
13-14.	Queensland Mus., J 1109, J 1110, Keppel Bay, mid-East Queensland — seen by Ogilby — "cannot be located in the present collections" — juveniles
15-16-17.	Queensland Mus., J 3066-68, Cape Bowling Green, mid-East Queensland — juveniles
18-19-20.	Queensland Mus., J 8551 (cast only), J 8575, J 8577, Thursday Island, Torres Strait — adult

*Specimens examined by E. E. Williams

[1] MCZ = Museum of Comparative Zoology; BM = British Museum (Natural History); FMNH = Field Museum of Natural History.

TABLE 1 (Cont.)

*21-30.	Australian Mus., R.8115-16, 8909-13, 9012, Sir Edward Pellew Group, Northern Territory — juveniles
*31.	Australian Mus., R.11756, Bathurst Island, Northern Territory — juveniles
*32.	Australian Mus., R.25691, Cape Don, Northern Territory — juvenile
33.	Western Australian Museum, R 773, Cape Don, Northern Territory — adult
*34-37.	Western Australian Museum, R 682-85, "N W Coast" — juveniles
*38-39.	Western Australian Museum, 10423-24, "from the Northwest" — juveniles
40.	Australian Mus., R.26347, Port Essington near Cape Don, Northern Territory — adult

TABLE 2

Frequency of postocular counts in *Chelonia mydas* from Tortuguero, Costa Rica; Ascension Island; and the Gulf of Baja California. In each pair of numbers heading the columns the first represents the left side and the second the right one.

	1-1	1-2	1-3	1½-2½	2-1	2-2	2-3	2½-3	2½-4	3-1	3-2	3-3	3-4	3-5	3½-4	4-2	4-3	4-4	4-5	4½-5	4-7	5-3	5-4	5-5	5-6	6-4
Tortuguero	2	2	2		3	3				1	5	77	70	3		2	88	409	85		1	1	118	65	2	1
Ascension Island													2					176					18			
Gulf of Baja California (data from Caldwell, 1962)				1		1	2	1	1		2	27	26	2	1		33	267	23	1			16			

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Figure 2. Distribution of *Chelonia depressa* in Australian waters.

Plate 1. *Chelonia depressa*, the British Museum hatchling. *Top:* dorsal view of head to show asymmetrical division of postparietal, and prefrontals equal in length to supraoculars. *Bottom:* dorsal view of body to show relative shortness of forelimbs and their weak scalation.

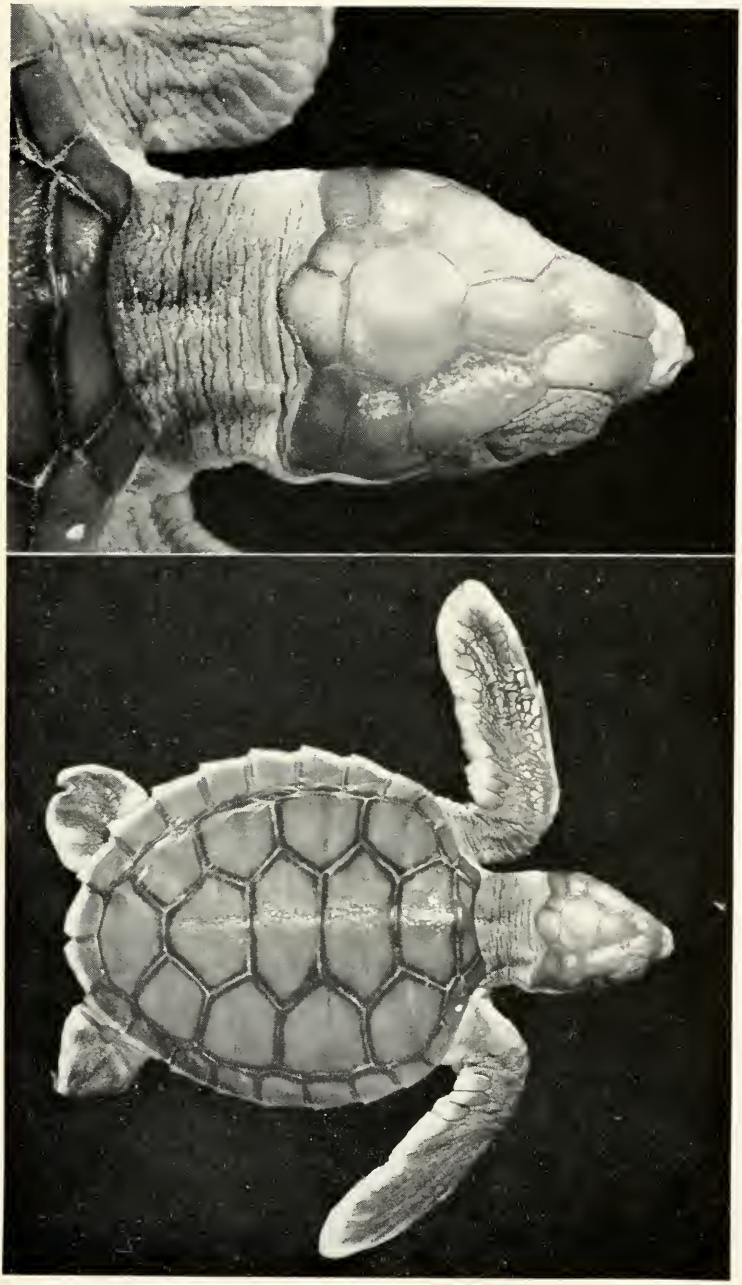
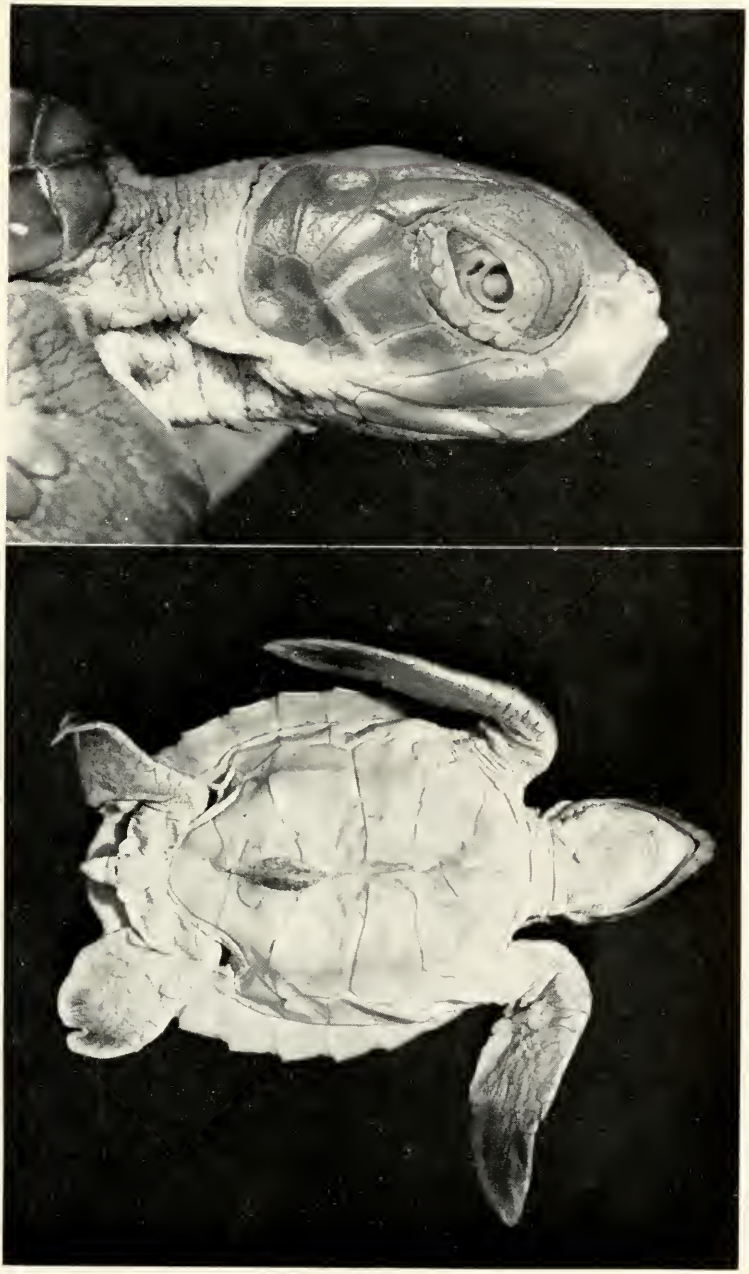


Plate 2. *Chelonia depressa*, the British Museum hatchling. *Top:* lateral view of head to show three postoculars and small number of subtemporal scales. *Bottom:* ventral view of body to show single brachial scale and weakness of scalation on forelimbs.



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THE ECOLOGICAL DISTRIBUTION OF THE ANOLINE LIZARDS AROUND KINGSTON, JAMAICA

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In each of the Greater Antilles and the islands of the Great Bahama Bank it is usual to find several species of *Anolis* very common in a small area. Though taken in the same habitat or even from the same tree, the species differ in where they live within the habitat. Differences in microhabitat have been described for the four species on Bimini by Oliver (1948); on Cuba for five species in Camaguey and Oriente by Ruibal (1961), and for five species near Havana by Collette (1961); for seven of the ten species on Puerto Rico by myself (Rand, 1964); and for the three commonest species on Hispaniola (Rand, 1962). No comparable study has been published for Jamaica, though the systematics of the anoline lizards have been described by Underwood and Williams (1959), and some notes on their ecology given by Grant (1940) and Underwood (1951). This paper attempts to fill this gap in our knowledge by presenting data on the differences in microhabitat among five Jamaican anoles. I restrict myself to the anoles near the city of Kingston because microhabitats do differ geographically in Jamaican anoles — particularly in *Anolis lineatopus*.

THE JAMAICAN ANOLES

Seven species of the genus *Anolis* are known from Jamaica: *Anolis valencienni, garmani, opalinus, grahami, lineatopus, reconditus,* and *sagrei.* The last of these, *sagrei,* occurs widely on Cuba and the Bahamas and may have been introduced by man into Jamaica. It is restricted to the west end of the island. *Anolis reconditus* is known from only a few specimens from the Blue

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Mountains and is closely related to *lineatopus*. The remaining five species are widespread on the island. According to Etheridge (1960), all five are quite closely related, and four of them, *garmani, opalinus, grahami,* and *lineatopus,* are more closely related to one another than they are to species occurring elsewhere. Among these four, *opalinus* and *grahami* are particularly close (Underwood and Williams, 1959).

Except for *sagrei,* only *grahami* occurs outside of Jamaica. It has been introduced into Bermuda, and a subspecies or related species occurs on Grand Cayman.

I have followed the nomenclature of Underwood and Williams except in considering *valencienni* a member of the genus *Anolis* rather than of *Xiphocercus*; in this I follow Etheridge cited in Williams (1962).

METHODS

The observations, summarized, on the ecological distribution of the five species of *Anolis* occurring in the vicinity of Kingston were made during a ten month stay.

Kingston, on the south coast of Jamaica, in the rain shadow of the Blue Mountains, has a climate which is tropical and semi-arid. Probably completely covered by forest or scrub originally (Asprey and Robbins, 1953), there are now no completely undisturbed areas in the vicinity of the city. Present habitats range from moderately tall forest through dense, thorny second growth to open grassy pastures, and include a variety of edificarian situations, including well-watered gardens and parks.

The distributions of the *Anolis* are not uniform through these habitats. Each species occupies a different microhabitat though these overlap widely and in some places all five species are present. I have seen four different species in one tree at the same time and individuals of two species within a few inches of one another. This overlap between species is striking and tends to obscure differences in their ecological distribution.

The microhabitats of species around Kingston differ in at least two ways: in the sorts of perches which they use, and in the sorts of habitats where they are common.

To show these differences, censuses were run in four different areas selected to cover the most frequent habitats around Kingston. Two of these areas were much modified by man, the other two less so.

The first area, "Barbican, open," was in a new residential suburb north of Kingston. This had recently been cleared of thorn scrub second growth and built up to new houses with moderate to extensive grounds. There were some small trees but few large ones, many fences, hedgerows, grassy lawns, and buildings. It was the most open area censused.

The second area, "Mona, park," was part of the grounds of the University of the West Indies at Mona, east of Kingston. This was park-like with quite well-kept lawns and many larger trees, most of these scattered and isolated from one another but some growing in small groves. There were not many smaller trees and relatively few bushes.

The third area, "Barbican, bush," was dense thorny scrub second growth joining the first area. There were scattered larger trees but most were only 15-30 feet tall with much undergrowth and many tangled vines. The ground was covered with dry leaf litter.

The fourth area, "Mona, bush," was taller forest at the base of Long Mountain near the second area. This was also second growth, though older than that at Barbican, and may never have been clean felled. There were many tall trees, 40-60 feet, forming a nearly complete canopy, and the undergrowth, though quite dense, was more open than in the Barbican second growth and in one place had been cleared completely leaving only the larger trees. There were many vines and a litter of dead leaves on the ground.

Each area was carefully searched repeatedly, and each lizard recorded where it was first seen. No area was censused more than once a day and a lizard was only counted once per census even if it changed its position radically.

Even with binoculars, many of the lizards present in an area were not seen, and those seen are not a random sample of those present. In all species the males are larger and more conspicuous than the females. Certain species are more easily seen than others. The large green *garmani* is more conspicuous than any other; the slow-moving grey *valencienni* is the least conspicuous. A lizard on a bare tree trunk at eye level is not apt to be overlooked, but one on top of a branch high overhead frequently escapes notice. The further up a lizard is, and the further out among the foliage, the less likely it is to be seen. Because of this bias, the census results are not fully valid representations of the distribution of the lizards, but since this bias acts equally for each species, the differences between them should be real. This

censusing technique and its weaknesses have been discussed more fully in my paper (Rand, 1964) on the *Anolis* of Puerto Rico.

Of the various possible characteristics of the lizards' perches, two were selected for analysis: the height above the ground at which each lizard was seen and the diameter of its perch.

The data on height of perch and perch diameter did not seem to vary significantly from habitat to habitat and these have been combined in Table 1. The statistical significance of the differences in perch height is given in Table 2. The abundance of the various species in the different habitats is given in Table 3.

In the following accounts of the species, the census data are supplemented by a summary of more casual observations on these species, both within and outside of the census areas.

OBSERVATIONS

Anolis lineatopus lineatopus

This form is moderate in size (males reaching 70 mm snout-vent length) and a strongly patterned brown in color. This is probably the most abundant species in the Kingston area and certainly the most commonly seen.

Anolis lineatopus occurs in the widest variety of habitats of all of the Kingston anoles. As Table 3 shows, it was common in all four census areas, but least common in the Mona bush. It was also common in old shady gardens, in fencerows through grazed pastures, and was the only species seen in the edge of the mangrove swamps on Palisadoes. It was quite commonly seen on porches and verandas and sometimes entered houses.

Like the other *Anolis, lineatopus* spends most of its waking time sitting on a perch. Unlike the others, it is commonly seen on a perch where it could not climb higher than a couple of feet. Individuals were seen on trees, on fence posts, on stone walls, on rocks both large and small, on ruined houses and on the walls of occupied dwellings, as well as in hedges and bushes. Of all the species it was most frequently seen on the ground (6 during census), though individuals spent only short periods there.

Most *Anolis lineatopus* recorded during censuses were close to the ground and on moderate to large diameter perches (Table 1). Seventy-six per cent were below 6 feet and about 83 per cent on perches larger than ½ inch. Large individuals (adult males) usually perched somewhat higher (only 26% below 3 feet) than did smaller individuals (adult females and sub-adults, 60% below 3 feet). This difference is significant at the 1 per cent level

(Table 3). The maximum height at which a large individual was seen during census was 9 feet. Individuals were rarely seen higher than this at any time. Larger *lineatopus* were less frequently seen on small diameter perches (13% on perches less than ½ inch) than were small ones (20% on perches less than ½ inch).

Very young *lineatopus* seemed to avoid larger trees and were usually seen close to the ground in bushes, hedges, brush piles, or sometimes perching on large dead leaves on the ground.

Anolis grahami grahami

This species is of moderate size (males reaching 70 to 75 mm snout-vent length), predominantly light green in color but can change to dark brown. There is also a common finely spotted phase.

Where it occurs, *grahami* may rival or even surpass *lineatopus* in abundance. However, as Table 3 shows, it is common only in the more open areas both at Mona and in Barbican, and quite rare in the bushy or forested areas. It occurs in grazed pastures. It was also common in the shady, well-watered gardens around Kingston as well as in the newer more open ones, and it was this species which most commonly entered houses, climbing on the walls and hiding behind pictures, though usually venturing outside the house during the day.

This species is most frequent on trees and walls and, when seen on fence posts and stones and in brush heaps, there is usually the opportunity to climb to a fair height. Individuals, particularly smaller ones, were not infrequently seen in hedges. Individuals were seldom seen on the ground and none during census taking.

Most *Anolis grahami* (Table 1) recorded during census were well above the ground and on moderate to large diameter perches. Sixty-six per cent were above 5 feet and 92 per cent on perches of a diameter greater than ½ inch. Large individuals (adult males) and smaller ones (adult females and sub-adults) show little difference (not significant at the 5% level, Table 2) in the height at which they were seen, though there is a curious and unexplained small number of smaller lizards seen between 6 and 10 feet. There is some tendency for smaller individuals to be seen on small diameter perches more frequently than are larger individuals.

The maximum height at which large individuals were seen during census was 25 feet, for smaller individuals 30 feet. Such heights were not infrequently seen during casual observations.

Very young *grahami* were seldom seen and usually were up well above the ground.

Anolis opalinus

This is a small species (adult males reaching between 45 and 50 mm snout-vent length), grey or brown in color, usually reticulated, with a prominent light lateral stripe.

Though quite common in the habitats which it occupies, it is much less conspicuous than either *grahami* or *lineatopus,* in part because of its small size and drab coloration and in part because it is less common around houses.

Anolis opalinus is primarily a lizard of bushy or forested areas. Grant reports that it is called "coffee lizard" for this reason. As Table 2 shows, it was completely absent from the residential area in Barbican and rarely seen in the park-like area in Mona. These census results are substantiated by other observations, and this species was never seen around the houses in Mona and Barbican and only rarely on the University of the West Indies campus at Mona, and then only in one group of tall trees, with dense foliage, grown close together and close to the forested area. It was quite common in both bushy study areas, less in the dense second growth at Barbican than in the more open and taller forest at Mona.

This species was never seen in open pasture situations around Kingston and curiously enough it was rare or absent in the old, well shaded gardens in the residential areas we examined.

Around Kingston, this species was almost always seen on trees or bushes, though sometimes on hanging vines. It was seldom seen on rocks, logs, or stumps even in the areas where it was quite common. It was also seldom seen on the ground and never so during censusing.

Most *opalinus* recorded during census were well above the ground and on moderate to large diameter perches (Table 1). Only 11 per cent were recorded below 3 feet and about 63 per cent were recorded above 5 feet. About 94 per cent were on perches of a diameter greater than ½ inch. Large individuals (adult males) and smaller ones (adult females and sub-adults) show somewhat similar distributions in height, though the difference is significant at the 1 per cent level (Table 2). More of the smaller individuals were seen on small diameter perches (11% on perches less than ½ inch) and were less frequently seen more than 6 feet above the ground.

No very young individuals were seen close to the ground.

Anolis garmani

This species is the largest of the Jamaican *Anolis* (males reach 120 mm in snout-vent length). It is usually bright green in color but can change to dark brown.

In the Kingston area this species is nowhere near as abundant as the three preceding species. An hour or two of searching was usually required to find even a single individual, and during most census periods none were seen at all. As Table 2 suggests, this species was most common in the bushy or forested areas, and it was seen during census in neither the open residential area at Barbican nor the park area at Mona. However, during casual observation, occasional individuals were seen in both these latter areas. Individuals of this species were never seen on isolated trees in open pastures, even on large trees. They were, however, seen occasionally in the older, shady, well-established gardens in Mona.

Though occasionally seen in bushes or vine tangles, and once on a telephone pole, most individuals were seen on large trees. Though they do occur in gardens occasionally, none were seen to enter houses or on stone walls or ruins. None were seen on the ground.

Data from individuals collected to determine temperatures have been added to those collected during censuses, in Table 1. The data are still meagre but suggest that *garmani* occurs primarily high in the trees, as 61 per cent of the records are over 6 feet and 44 per cent over 10 feet. All individuals seen were on moderate to large perches. These data accord with general observations that this species is one which lives well above the ground.

No very young individuals were seen.

Anolis valencienni

This species is second in size only to *Anolis garmani* (adult males reach about 80 mm snout-vent length). It is a mottled grey in color.

Though seldom seen and certainly less common than any species except *garmani,* this species occurs in a wide variety of habitats. It is very cryptically colored and usually slow moving so that it is seldom seen and is certainly more common than the census figures indicate. As Table 2 shows, it was taken in Mona both in the park area and in the forest. None were seen during censusing at Barbican but during casual observations they were noted occasionally in both the open residential area and in the dense second growth. Almost everywhere we watched *Anolis,*

this species eventually turned up — except in the mangroves and in the open pastures. It certainly occurred in the old established gardens in the residential areas.

This species was almost always seen on trees, though one was seen on a fence post, and occasionally in taller bushes. This species is most unlike the others in its movements and posture for it is a slow-moving animal which spends much of its time pressed close to its perch.

The few census records (to which have been added data collected during temperature studies) show that this species occurs over a wide range of heights and with a less clear height preference than the other species (Table 1). The census data suggest that it uses mostly moderate to large diameter perches. This is the only point where my casual impressions contradict the census results. My impression, based on casual sightings and on watching individuals, is that this species spends much of its time out among the smaller branches and twigs far from the trunk, and that in this it differs from the other species.

The few very young individuals seen were on trees and bushes several feet above the ground.

DISCUSSION

A comparison of the three common species of *Anolis* in the Kingston area shows that each occupies a different microhabitat, though overlap occurs between them.

These differences are of two types, differences in the usual perch height and differences in the type of habitat occupied.

Each species of *Anolis* spends most of its time on certain kinds of perches. The characteristics which these perches have in common describe the structural niche of the species. Important among these characteristics is perch height. The types of habitats frequented by a species seem related to the amount of sun available and in turn to temperature. This aspect of the distribution can be called a climatic niche. These terms have been discussed at greater length with respect to the *Anolis* of Puerto Rico (Rand, 1964).

In perch height, (Table 1), *lineatopus* differs from both *grahami* and *opalinus* in perching closer to the ground, while *grahami* and *opalinus* are almost identical in their perch height distribution. Table 2 shows the differences between male *lineatopus* and male *grahami,* female *grahami,* and male *opalinus* significant at the 0.1 per cent level. The differences between female *lineatopus*

and both sexes of *opalinus* and *grahami* are significant at the 0.1 per cent level. The differences between *grahami* and *opalinus* are nowhere significant at the 1 per cent level, though that between female *grahami* and female *opalinus* is significant at the 5 per cent level. Though there are differences among these species in another aspect of structural niche, i.e. perch diameter, these are small and probably of much less importance.

The difference in perch height is probably more important than these figures indicate. Much of the food which *lineatopus* catch is on the ground, while the food of the other two species tends instead to be insects which are either on the lizard's perch or on nearby branches or leaves.

Two of these three species show intraspecific differences in perch height. In both *lineatopus* and *opalinus* small individuals perch closer to the ground than do large ones. The difference in *lineatopus* is striking, in *opalinus* less so. Where these two species occur together the intraspecific differences assure that the greatest overlap between them involves the large individuals of the larger species (*lineatopus*) and the small individuals of the smaller species (*opalinus*). Those individuals which are closer in size, large *opalinus* and smaller *lineatopus,* overlap least.

In *grahami* there is a slight tendency for the smaller individuals to range higher than do the large ones, so that where *grahami* and *lineatopus* occur together the overlap is greater between the large individuals (adult males) of each species and less between the smaller individuals (females and sub-adults). A study of the social behavior of *lineatopus* (Rand, 1967) has shown that adult males have much larger territories (defended home ranges) than do females and sub-adults. *A. grahami* behave similarly. It was also found that female *lineatopus* and *grahami* defend their territories against other lizards of their own size regardless of species while the males seem to be more tolerant of other species. Where *lineatopus* and *grahami* occur together, the overlap is greatest between the individuals with the largest home ranges and least between those with the smaller home ranges. The spatial separation between the smaller *grahami* and *lineatopus* may be reinforced by their interspecific territorial defense.

The other differences between these three species are in the habitats which they occupy. *Anolis lineatopus* occurs throughout the habitats studied around Kingston and so overlaps completely the other two species. However, *opalinus* and *grahami* occupy quite different habitats and show relatively little overlap. In general, *opalinus* occurs in bushy or forested areas while

grahami occurs in more open areas and in gardens. Differences of this sort between other species of *Anolis* on other islands have been correlated with differences in amount of shade and with the preferred temperatures of the lizards, by Ruibal (1961) for several Cuban species, and by Rand (1964) for the Puerto Rican species.

Certainly the forested areas where *opalinus* is most common are more shaded than the open areas where *grahami* occurs. Some very scant data on temperature indicate that these areas are also cooler. Rand (1964) found that in Puerto Rico the species which lived in the shade at low elevations ranged much higher into the mountains than did the species which lived in the sun at low elevations. In Jamaica, *opalinus* reaches much higher elevations than does *grahami* (Underwood and Williams, 1959).

Data on the body temperatures of these three species were collected at Kingston. Lizards were noosed and their cloacal temperatures taken with a Schulthies Museum Special Thermometer, within a few seconds after capture. The temperature of the air was then taken in the immediate vicinity. Temperatures were taken only during sunny periods when the lizards had the opportunity to thermoregulate. These data are shown in Figure 1. This figure shows that *grahami* has an appreciably higher body temperature than does *opalinus*. This suggests that the difference between them in habitat distribution may be associated with their different temperature preferences, *opalinus* with a lower body temperature preference living in more shaded forest areas and *grahami* with a higher preferred body temperature living in more open, sunnier areas. The occurrence of *grahami* and not *opalinus* in some of the very shady gardens in residential areas does not fit this picture but may be due to the small extent of each garden.

The body temperature of *lineatopus,* whose habitat range overlaps those of both the other two species, might be expected to be intermediate. It is clearly lower than that of *grahami*. Associated with this is the fact that it becomes active earlier in the morning than does *grahami* and even more noticeably moves out of the sun earlier in the day. The *opalinus* temperatures appear lower than those of *lineatopus,* though too few to be really conclusive.

To summarize, the three common species of *Anolis* in the Kingston area differ from one another in their ecological distribution. One species, *Anolis lineatopus,* differs from the other two in one aspect of its structural niche, living much closer to the ground than do the other two. These two have very similar structural niches but one of them, *opalinus,* lives in the forested areas

and the other, *grahami,* in the more open areas. *A. opalinus* has a lower preferred body temperature than does *grahami,* which suggests that the difference between them is one of a climatic niche.

The relationships of the two rarer species of *Anolis, garmani* and *valencienni,* between themselves and to the three common species, are less well documented than are the relationships among the three common species.

The largest species, *garmani,* lives high in trees and thus seldom comes in contact with *lineatopus.* The difference in perch height between male *lineatopus* and *garmani* is significant at the 1 per cent level; between smaller *lineatopus* and *garmani* at the 0.1 per cent level (Table 2). Like *opalinus, garmani* is most common in the forested or bushy areas and avoids the more open areas, though it occurs in shaded gardens with *grahami.* There is a suggestion that *garmani* lives even higher in the trees than do *opalinus* and *grahami,* and also that it is much more closely restricted to large trees than they are. It is probable that in *Anolis* the size of the prey caught is strongly correlated with the size of the lizard (Schoener, 1967). It, therefore, may be important that the two species which overlap most widely (*garmani* and *opalinus*) are the most different in size, *garmani* being the largest of the Jamaican species and *opalinus* the smallest.

The census data on the final species, *A. valencienni,* suggest that this species overlaps both the climatic and structural niches of all of the other species, though overlapping *lineatopus* least. However, the census data are few and, as mentioned before, I have a strong impression that this species spends much more time out among the smaller branches than do any of the others. It is rather different from the other species in its slow motion and in its appearance, and Underwood (1951) reports: "I have kept alive a number of these lizards, and it seems to me that they prefer somewhat larger insects than do other anoles of comparable size."

The situation described for Kingston seems to be repeated all along the dry south coast of Jamaica from about the Morant River in the east nearly to Mandeville in the west and a short way up into the foothills of the mountains. A similar situation may exist on the north coast from about Port Antonio west to near Lucea. However, over the rest of the island the situation is complicated by the replacement of *A. l. lineatopus* by other forms of *A. lineatopus* with rather different habitat preferences. Unfortunately, there is not enough information to describe these situations adequately.

The Jamaican anoles can be compared with those of Puerto Rico (Rand, 1964), an island of comparable size and with a similar number of species, but ones that are only very distantly related to those on Jamaica (Etheridge, 1960), the Jamaican animals belonging in the beta section of the genus while the Puerto Rican species are members of the alpha section.

With respect to the structural niche, two Puerto Rican species (*A. cristatellus* and *gundlachi*) are very similar to *A. lineatopus;* two species (*A. evermanni* and *stratulus*) are very similar to *A. opalinus* and *grahami;* and one species (*A. cuvieri*) is apparently like *A. garmani.* There is on Puerto Rico no species comparable to *A. valencienni* in structural niche, while on Jamaica there is no species comparable to the Puerto Rican grass and twig living species *A. krugi, pulchellus* and *poncensis.*

As in Jamaica, the most closely related Puerto Rican species occupy similar structural niches but differ in microclimatic niches. In Puerto Rico, two pairs of species and a triplet do this, while in Jamaica only one (possibly two) such pair exists. The ecritic temperatures of the Puerto Rican species are similar to those of their Jamaican counterparts but not identical.

Thus the anoline faunas of these two islands, though only distantly related, show similarities in their microhabitats. Certain of the structural and climatic niches occupied on both Jamaica and Puerto Rico are very similar. Even more striking is the similarity in the kinds of differences in microhabitats between anoles. On each island very closely related species are paratopic or nearly so and differ in climatic niche and ecritic temperature, while syntopic species are less closely related and usually occupy different structural niches. There has been considerable parallelism in at least certain of the ecological aspects of the independent adaptive radiations of the *Anolis* on Puerto Rico and on Jamaica.

ACKNOWLEDGMENTS

I am indebted to Professor David Steven and the staff of the Zoology Department of the University of the West Indies for allowing me to use their facilities and for helping me in many other ways during my stay in Jamaica. I must also thank Dr. E. E. Williams for his advice and criticism throughout this project, and my wife Patricia for her help both in the field and in preparing the manuscript. This study was supported in part by National Science Foundation Grant No. G-16066.

SUMMARY

During a ten month field study in the vicinity of Kingston, Jamaica, four different habitats were censused for comparative data on perches used (structural niches) and habitats occupied (climatic niches) by five species of *Anolis*.

In the Kingston area there are three very common species: *lineatopus, opalinus*, and *grahami*.

Anolis lineatopus lives near the ground on moderate to large diameter perches, female and young perching lower and on smaller perches than adult males. It ranges from the most densely forested through the most open habitats. The eccritic temperature range seems intermediate between those of the following species.

The closely related species *A. opalinus* and *grahami* both use moderate to large perches and perch higher than does *lineatopus*. *A. opalinus* lives in forest and *grahami* in the more open habitats. They replace one another with relatively little overlap. *A. grahami* has a higher eccritic temperature range than does *opalinus*.

Of the two less common species, *A. garmani* lives high in trees in the forest. This is the largest of the Jamaican species and it may be significant that the common species that it overlaps most widely is the smallest, *opalinus*.

Anolis valencienni ranges through all habitats and occurs on a variety of perches, probably most frequently on the branches of the crown. This species differs from the others in shape and in its slow movements, and there is some indication that it also takes larger prey.

Though the Jamaican anoles are only distantly related to those of Puerto Rico and represent the results of independent adaptive radiations, there has been considerable parallelism in the partitioning of the habitat with respect to both structural and climatic niches on the two islands.

TABLE 1

Structural niche distribution in Kingston anoles based on data collected during the censuses described on page 2. The number of individuals seen is expressed as a percentage of the total number of individuals of that species (and size group in the first three species).

Anolis lineatopus

Perch height	Perch diameter	Large individuals N=77 >3″	½-3″	<½″	leaf	Total	Smaller individuals N=78 >3″	½-3″	<½″	leaf	Total
	>10 ft	5.2%	1.3	1.3		7.8					
	6-10 ft	7.8	15.6	6.5		29.9	7.7%	1.3	1.3		10.3
	3- 5 ft	20.8	11.7	3.9		36.4	12.8	16.7			29.5
	< 3 ft	11.7	13.0		1.3	26.0	24.4	16.7	19.2		60.3

Anolis grahami

	Large individuals N=62 >3″	½-3″	<½″	leaf	Total	Smaller individuals N=40 >3″	½-3″	<½″	leaf	Total
>10 ft	19.4%	9.7	1.6		40.7	27.5%	10.0			37.5
6-10 ft	25.8	9.7	1.6		37.1	2.5	12.5	10.0		25.0
3- 5 ft	14.5	8.1			22.6	20.0	5.0	2.5		27.5
< 3 ft	6.5	3.2			9.7	5.0	2.5		2.5	10.0

Anolis opalinus

	Large individuals N=46 >3″	½-3″	<½″	leaf	Total	Smaller individuals N=64 >3″	½-3″	<½″	leaf	Total
>10 ft	13.0%	23.9			36.9	4.7%	9.4			14.1
6-10 ft	28.3	10.9			39.2	15.6	15.6	7.8		39.0
3- 5 ft	6.5	6.5			13.0	21.9	12.5	1.6		36.0
< 3 ft	10.9				10.9	6.2	3.1	1.6		10.9

Anolis garmani

	All individuals N=18 >3″	½-3″	<½″	leaf	Total
>10 ft	33.3%	11.1			44.4
6-10 ft	11.1	5.6			16.7
3- 5 ft	11.1	11.1			22.2
< 3 ft	11.1	5.6			16.7

Anolis valencienni

	All individuals N=23 >3″	½-3″	<½″	leaf	Total
>10 ft	17.4%	4.3	4.3		26.0
6-10 ft	17.4	8.7			26.1
3- 5 ft	17.4	13.0			30.4
< 3 ft	13.0	4.3			17.3

TABLE 2

Statistical significance of differences in perch height in Kingston *Anolis*. Chi squares calculated by P. E. Vanzolini.
Significance level: * = 5%, ** = 1%,
*** = 0.1%.

		lineatopus		*grahami*		*opalinus*		*garmani*	*valencienni*
		large	smaller	large	smaller	large	smaller		
lineatopus	large	24.630 ***		17.556 ***	17.059 ***	22.743 ***	6.289	15.618 **	5.750
	smaller			59.108 ***	48.510 ***	60.512 ***	16.462 ***	40.800 ***	30.027 ***
grahami	large				1.683	1.674	5.884	3.184	1.981
	smaller					3.595	7.862 *	1.125	1.247
opalinus	large						11.252 **	3.219	4.257
	smaller							9.496	2.923
garmani									1.661

TABLE 3

Habitat distribution: the number of Kingston *Anolis* seen in four different habitats during a series of censuses.

	lineatopus	*grahami*	*opalinus*	*garmani*	*valencienni*
Barbican, open (Residential area)	44	20	0	0	0
Mona, park (UWI Campus)	65	69	2	0	5
Barbican, bush (Dense second growth)	52	3	25	4	0
Mona, bush (Tall second growth)	19	5	77	7	3

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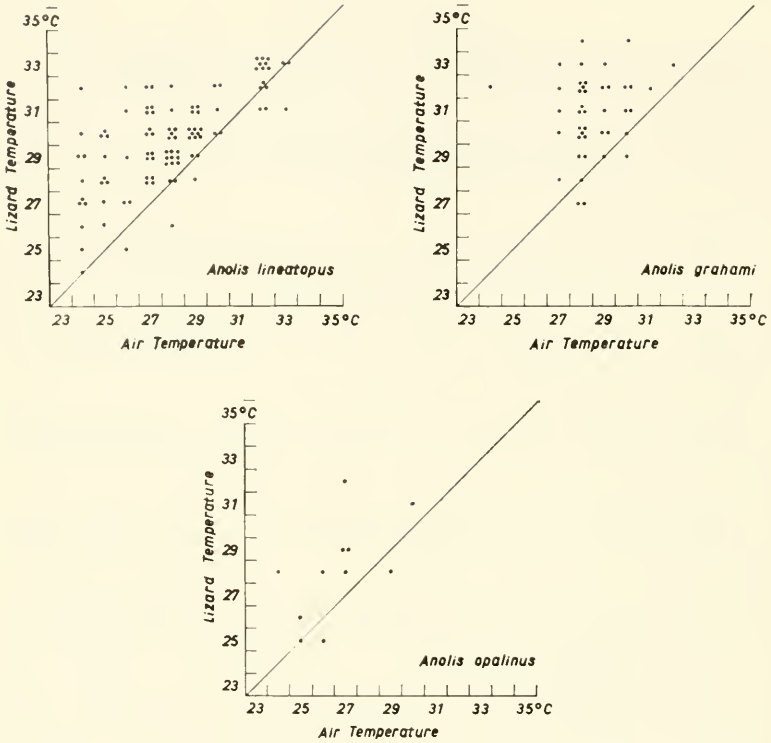

Figure 1. Anole body temperature plotted against ambient air temperatures.

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STUDIES ON NEOTROPICAL POMPILIDAE (HYMENOPTERA) III. ADDITIONAL NOTES ON *EPIPOMPILUS* KOHL

Howard E. Evans

Epipompilus is one of the more exciting genera of Pompilidae, not only because these are among the most brilliantly colored of spider wasps, but also because of the many unusual and apparently primitive structural features of the genus. A few years ago the group was known from about six specimens, all females. In 1961 (Psyche, 68: 25-37), I described the male and reviewed the American species, basing my review on 18 specimens representing nine species. I have now accumulated more than 100 specimens and feel in a position to make some important additions to knowledge of the genus. Three species are described as new, all from South America, and the males of three species are described for the first time (*nigribasis, aztecus,* and *pulcherrimus*). The last-named species is the only one known from the United States, and I am indebted to R. W. Dawson of Washington State University for sending me an excellent series collected at the Archbold Biological Station in Florida. For much new South American material I am indebted to Fritz Plaumann, of Nova Teutonia, Brazil, and to Charles C. Porter of Harvard University.

Thirteen American species of *Epipompilus* are now known. Seven of these are known from both sexes, five from females only, and one from males only. All species are included in the following key, but only those species are discussed in the text which are described as new or for which new information is available. I have placed the species in two groups on the basis of an apparent concordance of the shape of the male subgenital plate with the nature of the convergence of the eyes of the female. I am hopeful that this may assist in making future sex associations.

KEY TO SPECIES

Females

1. Eyes converging at the top, the upper interocular line distinctly less than the lower interocular line; front fairly wide, middle interocular line at least about 0.57 x width of head (*aztecus* group) 2
   Eyes parallel or diverging above, the upper interocular line equal to or exceeding the lower; front barely wider than the two eyes taken together, middle interocular line at most about 0.55 x width of head (*delicatus* group) 6
2. Wings wholly fuliginous; abdomen wholly rufous; middle and hind tibiae with numerous short spines above .....
   .....*pulcherrimus* (Evans)
   Wings hyaline, bifasciate; abdomen black with whitish spots; middle and hind tibiae not or exceedingly weakly spinose 3
3. Abdomen with whitish spots only on tergites two and five, none on sternites .....*aztecus* (Cresson)
   Abdomen with whitish spots on tergites two through five or six, also on some of the sternites 4
4. Greater part of thorax and propodeum rufous; apical tergite black .....*bifasciatus* (Ashmead)
   Greater part of thorax and propodeum black; apical tergite with whitish markings 5
5. Pronotum entirely rufous; hind femora black; propodeum, in profile, nearly flat in front, obliquely declivous behind .....*inca* n. sp.
   Pronotum mostly black, with a whitish band along the posterior margin and with whitish and rufous markings anteriorly; hind femora ferruginous; propodeum, in profile, forming a smooth arc .....
   .....*jocosus* n. sp.
6. Body and legs wholly black except for a pair of small whitish spots on second tergite; pronotum short, subangulate behind .....
   .....*williamsi* (Banks)
   Body and legs variously marked with rufous and whitish; pronotum arcuate or very weakly subangulate behind 7
7. Thorax wholly rufous (or with limited black markings on sides of pronotum or on venter) (Central and South American species)
  8
   Thorax with extensive black markings (South American species) ....
  10
8. Front angle of ocellar triangle less than a right angle, postocellar and ocello-ocular lines subequal; second abdominal tergite yellowish brown .....*insolitus* Evans
   Front angle of ocellar triangle greater than a right angle, postocellar line much exceeding ocello-ocular line; second tergite with a whitish band or spots 9

9. Postnotum a very narrow band; face and clypeus testaceous, antennae wholly testaceous; length of fore wing under 4 mm ..... *nigribasis* (Banks)
Postnotum medially about half as long as metanotum; face and clypeus black, antennae infuscated on apical third; length of fore wing 5-6 mm ..... *delicatus* Turner

10. Tergites one and two mostly black, the latter with white markings; pronotum with extensive pale markings; postocellar line only slightly exceeding ocello-ocular line ..... *tucumanus* n. sp.
Basal 1.5-2.5 tergites rufous, second sometimes with white markings; pronotum wholly black; postocellar line much exceeding ocello-ocular line 11

11. Propodeum black except for limited whitish markings; antennae black; radial vein angulate at second intercubital vein ..... *haupti* (Arlé)
Propodeum ferruginous; antennae ferruginous except darker apically; radial vein arcuate ..... *excelsus* (Bradley)

Males

1. Subgenital plate with a broad, truncate base from which arises a slender, parallel-sided spine-like process (as in Figs. 1, 3); known species either with the thorax extensively ferruginous or the femora and tibiae almost wholly ferruginous (*aztecus* group) 2
Subgenital plate tapering gradually to a point from a relatively narrow base (as in Fig. 5); known species without ferruginous markings on the thorax and with the hind legs, at least, mostly fuscous (*delicatus* group) 5

2. Length of fore wing 4.5 mm or less; transverse median vein of hind wing erect, nearly perpendicular to anal and median veins; body black except clypeus and pro- and mesonota contrastingly ferruginous ..... *pulcherrimus* (Evans)
Length of fore wing 5.5 mm or more; transverse median vein of hind wing oblique; body color not as above 3

3. Thorax black, with limited whitish markings on pronotum and propodeum; hind femora ferruginous; aedoeagus very long and slender (Fig. 2) ..... *jocosus* n. sp.
Thorax in considerable part rufous; hind femora black; aedoeagus not as above 4

4. Wings strongly twice-banded; middle legs mostly fuscous; basal third of antennae light ferruginous ..... *aztecus* (Cresson)
Wings weakly once-banded; middle femora and beyond light reddish brown; antennae brownish basally ..... *innubus* Evans

5. Eyes strongly hairy; length of fore wing not over 3 mm; aedoeagus exceedingly short (Fig. 6) ..... *nigribasis* (Banks)
Eyes with very short, barely noticeable hairs; length of fore wing over 3 mm; aedoeagus longer than above 6

6. Front coxae with at least the basal 0.4 black; mesopleura rather dull, the punctures coarse, separated for the most part by less than their own diameters; parameres slender, somewhat tapering (Brazil) .... *excelsus* (Bradley)

Front coxae with at most the basal 0.3 black; mesopleura shining, finely punctate; parameres broader and more coarsely setose 7

7. Third submarginal cell barely wider than high; parameres blunt apically, volsellae moderately slender (Central America) *delicatus* Turner

Third submarginal cell much wider than high; parameres acute apically, volsellae unusually slender (Argentina) ..... *tucumanus* n. sp.

AZTECUS SPECIES-GROUP

Epipompilus pulcherrimus (Evans)

This species has been known from two females, one from southern Florida and the other from Andros Island in the Bahamas. R. W. Dawson collected one female and five males in a Malaise trap at the Archbold Biological Station, Lake Placid, Florida, in the winter of 1965-1966 (29 Oct.-Jan. 6). The female is small (fore wing 4.5 mm) and differs from the two females previously known in having the pronotum wholly black except the collar, the remainder of the thorax and propodeum wholly black.

Description of male. — Length 4.5-5.0 mm; fore wing 3.5-4.5 mm. Head black except clypeus and mandibles in large part testaceous; antennae black; palpi brown; thorax black except entire pronotum, mesoscutum, and scutellum bright ferruginous (these areas with some black blotching in one specimen); legs black except all spurs whitish, front femora and tibiae suffused with testaceous, hind tibiae with a basal white spot; wings clear hyaline, with dark veins and stigma. Body clothed with short, whitish hairs, these hairs rather long on posterior slope of propodeum.

Clypeus truncate, twice as wide as high. Head 1.15 X as wide as high; front broad for the genus, middle interocular line 0.62-0.65 X width of head; eyes rather weakly convergent below, lower interocular line 0.95 X upper interocular line; ocelli in a broad triangle, postocellar line about 1.5 X ocello-ocular line. Front strongly alutaceous, with shallow but rather large, setigerous punctures. Antennae compact, segments five and beyond slightly produced below, so that the flagellum is crenulate in profile; first four antennal segments in a ratio of about 16:6:11:10, segment three about 1.5 X as long as thick. Setae of eyes exceedingly small. Pronotum short, its posterior margin arcuate; mesonotum closely

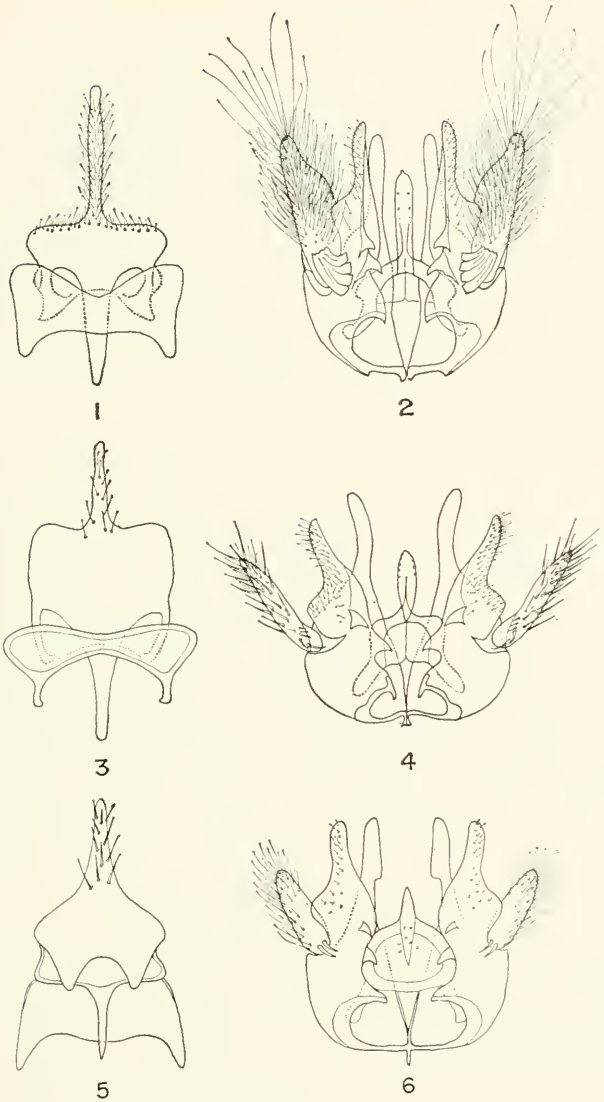

Fig. 1. Subgenital plate of male *Epipompilus jocosus* n. sp., paratype. Fig. 2. Genitalia of same specimen, ventral aspect. Fig. 3. Subgenital plate of male *E. pulcherrimus* (Evans). Fig. 4. Genitalia of same specimen, ventral aspect. Fig. 5. Subgenital plate of male *E. nigribasis* (Banks). Fig. 6. Genitalia of same specimen, ventral aspect.

punctate; postnotum nearly as long as metanotum, polished, depressed and slightly contracted medially. Propodeum shining, the setigerous punctures small; slope of profile low and even. Middle and hind tibiae with numerous short spines above; claws with a weak, erect tooth, except front tarsal claws more strongly toothed, the tooth subparallel to the outer ray, the outer claws of the front tarsus strongly curved. Fore wing with basal vein arising well beyond transverse median vein; radial vein arcuate, with only a faint angulation at the second intercubital vein; hind wing with transverse median vein erect, nearly perpendicular to anal and median veins, anal lobe large for the genus, half the length of the submedian cell. Abdomen rather small, depressed; subgenital plate in the form of a slender, setigerous process arising from a broad plate (Fig. 3); genitalia as shown in Figure 4.

Epipompilus aztecus (Cresson)

This species has been known only from southern Mexico. I have recently studied a male from Guatemala which represents the first known male of this species, as well as two females from Panama. The two females were collected on Barro Colorado Island, Canal Zone, one in April 1926 by C. T. Greene and one in May 1939 by J. Zetek [both U. S. National Museum]. They are relatively small for this species (fore wing 7.5-8.0 mm) and somewhat darkly colored: the middle femora are fuscous, and the propodeum and metapleura are wholly fuscous in one specimen, fuscous except at the anterior margin in the other. The male is from Santa Adelaida, Guatemala, collected at 1000 meters elevation in March and April, 1931, by J. Bequaert [coll. of Mus. Comp. Zool.]. All three of these specimens were borrowed many years ago by the late R. R. Dreisbach and have only recently become available for study. Dreisbach made a slide of the male terminalia, but it was poorly prepared, and in my opinion the subgenital plate on the slide (and perhaps the genitalia) do not properly belong with this specimen. I have therefore omitted mention of the terminalia in the short description that follows.

Description of male. — Length 7.0 mm; fore wing 5.7 mm. Head black, except lower inner orbits with a whitish streak, antennal sockets, face below sockets, and clypeus wholly light ferruginous; mouthparts largely light ferruginous, basal segments of maxillary palpi slightly infuscated; antennae ferruginous, apical two-thirds somewhat infuscated on upper surface; pronotum, mesoscutum, scutellum, upper half and posterior margin of mesopleura, and a small blotch on the metapleura, light ferruginous,

remainder of thorax and propodeum fuscous (posterior corners of propodeal rim white; disc of scutellum and lateral posterior margins of scutum slightly infuscated); front legs wholly light ferruginous, middle and hind legs fuscous except spurs white, tibiae with a white spot, and posterior coxae with a large white apical spot; abdomen fuscous, shining; fore wings strongly twice-banded much as in female. Body clothed with short, whitish hairs, these hairs rather coarse and conspicuous on the front and on the posterior part of the propodeum.

Clypeus large, measuring 1.85 X as wide as high. Head 1.12 X as wide as high, the vertex between the eyes forming a rather strong arc; front broad, middle interocular line 0.60 X width of head; inner orbits strongly convergent below, lower interocular 0.78 X middle interocular line, 0.93 X upper; ocelli in a broad triangle, postocellar line twice the ocello-ocular line. Front dull, with subcontiguous punctures on an alutaceous background. Antennae moderately long for the genus, weakly crenulate in profile; first four segments in a ratio of about 17:6:10:10, segment three 1.6 X as long as thick. Eyes not hairy. Pronotum short, with an abrupt anterior declivity, its posterior margin arcuate; mesonotum dull, closely punctate; postnotum considerably shorter than metanotum; propodeum with a strong median impression, in profile the slope very low. Hind tibiae with a few weak spines which barely extend above the pubescence; tarsal claws as described for *pulcherrimus*. Fore wing with the basal vein arising very slightly beyond the transverse median vein; radial vein slightly angulate at second transverse cubital vein; maximum width of third submarginal cell 1.6 X its maximum height; hind wing with transverse median vein oblique; length of anal lobe about 0.4 that of submedian cell.

Epipompilus bifasciatus (Ashmead)

This species has been known only from the type female from Bahia, Brazil. I have recently studied a second specimen from a locality not far distant: Corema, Paraiba, Brazil, June 1957 (no collector given) [coll. Dept. Zool., Sec. Agricultura, São Paulo]. It is slightly smaller than the type (fore wing 7.4 mm), but there are no important differences in color or structure.

Epipompilus jocosus new species

Holotype. — ♀, URUGUAY: Florida, Feb. 1952 (no collector stated) [MCZ, No. 31321].

Description of type female. — Length 9.5 mm; fore wing 7.5 mm. Head black, except mandibles, clypeus, and lower half of front light ferruginous, the ferruginous extending up the inner orbits to their point of greatest emargination; lower outer orbits, malar space, and labium also ferruginous, the palpi partially infuscated; pronotum black, except collar whitish and posterior margin with a whitish band (including the posterior lobes), the anterior margin, laterad of the collar, ferruginous; remainder of thorax and propodeum black, except for paired whitish spots just above the middle and hind coxae; abdomen black, with paired ivory-white spots on tergites two through six and sternites two through five, all of these spots partially or completely enclosing a black spot within them; antennae and front legs wholly ferruginous except somewhat dusky apically; middle and hind coxae black with whitish apices; middle and hind femora and middle tibiae ferruginous; hind tibiae fuscous, middle and hind tarsi dusky ferruginous; middle and hind tibiae with whitish spots near the base, tibial spurs whitish. Wings hyaline, the fore wing with two prominent brownish bands. Body uniformly clothed with pale pubescence.

Clypeus shallowly emarginate, measuring about 2.5 X as wide as high. Head 1.23 X as wide as high; eyes covered with short hairs; front moderately broad, middle interocular line 0.60 X width of head; eyes convergent above, lower interocular line 1.1 X upper; ocelli in a broad, flat triangle, postocellar line 2.2 X ocello-ocular line. First four antennal segments in a ratio of about 20:8:18:21, segment three 0.47 X upper interocular line. Front shining, closely punctate. Pronotum fairly long, broadly subangulate behind; mesoscutum closely punctate; postnotum wholly concealed dorsally; propodeum, in profile, smoothly convex. Front femora weakly incrassate; middle and hind tibiae with some very short spines intermingled with the pubescence; claws with the tooth long, erect. Fore wings with the radial vein quite strongly angled at the second intercubital vein, hind wing with the transverse median vein oblique, the submedian cell very sparsely and weakly setose, the anal lobe about 0.3 as long as the submedian cell.

Allotype. — ♂, BRAZIL: Nova Teutonia, Santa Catarina, 23 Feb. 1961 (F. Plaumann) [Mus. Comp. Zool.].

Description of allotype male. — Length 8.5 mm; fore wing 7.5 mm. Body black, with a bluish cast, marked with ivory-white as follows: apical three-fourths of mandibles, apical half of clypeus, spots on inner orbits opposite bases of antennae, pronotal

collar, band along posterior margin of pronotum, interrupted medially, sides of posterior rim of propodeum, apical margin of last abdominal tergite; antennae ferruginous, first two segments black above, flagellum moderately infuscated above, especially apically; coxae black, with apical white markings; trochanters black; femora ferruginous, tibiae also of this color except middle and hind tibiae infuscated at extreme base and toward apex and with a whitish spot on the outer side near the base; spurs whitish; tarsi fuscous. Wings lightly tinged with brownish, with a faint darker cloud in the marginal and second and third submarginal cells, also at the extreme wingtip. Body pubescence light brown to silvery, especially long and semierect on posterior slope of propodeum.

Clypeus weakly emarginate, 2.1 X as wide as long. Head 1.16 X as wide as high, the vertex arched very weakly above the eye tops; front narrow, middle interocular line 0.58 X width of head; inner orbits weakly convergent below, lower interocular line 0.95 X upper; ocelli in a broad triangle, post-ocellar line 1.7 X ocellio-ocular line. Eyes with only extremely short, inconspicuous setae. Front alutaceous and uniformly punctate. Antennae rather long, the flagellum crenulate in profile; first four segments in a ratio of about 17:7:14:13, segment three 1.8 X as long as thick. Pronotum of moderate length, broadly subangulate behind; mesoscutum closely punctate; postnotum shining, depressed medially, about two-thirds as long as metanotum; slope of propodeum low and even, the median line weakly impressed. Middle and hind tibiae with a large number of short spines above; tooth of claws strong, sloping outward somewhat, outer claws of front tarsus strongly curved, bifid. Features of wings as in female, except anal lobe of hind wing larger, about 0.4 as long as submedian cell. Subgenital plate and genitalia as shown in Figures 1 and 2; the very long setae at the apex of the parameres protrude from the apex of the abdomen even when the genitalia are in resting position.

Paratypes. — BRAZIL: 3 ♂ ♂, same data as allotype except dated 10-15 Feb. 1964, Jan. 1965 (F. Plaumann) [Mus. Comp. Zool., U. S. Nat. Mus.].

Variation. — The paratypes resemble the allotype closely in color except that one of them has the whitish band on the pronotum obsolescent. The fore wing varies from 6.5 to 7.7 mm in length; the middle interocular line varies from 0.56 to 0.59 X the head width, the lower interocular line from 0.85 to 0.95 X the upper interocular line.

Epipompilus inca new species

Holotype. — ♀, PERU: Machu Picchu, 1900 meters, 4-19 Sept. 1964 (C. C. Porter) [MCZ, No. 31322].

Description of type female. — Length 13.5 mm; fore wing 11 mm. Head black except lower inner orbits with a whitish streak, apical third of clypeus testaceous, mandibles testaceous except darker apically, palpi fuscous; pronotum wholly ferruginous; remainder of thorax and propodeum black except for paired small whitish spots on lower posterior angles of mesopleura and on upper metapleura, and much larger spots at the posterior angles of the propodeum; abdomen black, with large, paired whitish spots on tergites two through six and on sternites two through four, with much smaller spots on the last two sternites; antennae ferruginous, somewhat dusky apically; front legs ferruginous, the tarsi dusky; middle and hind coxae black, with white apices; middle femora ferruginous, the middle tibiae ferruginous except for a black streak on the outer surface; hind femora and tibiae black, the middle and hind tarsi also nearly black; hind tibiae with white spots near the base; tibial spurs dusky ferruginous. Wings hyaline, fore wing with two prominent brownish bands. Entire body clothed with short, pale pubescence.

Clypeus shallowly emarginate, measuring about 2.5 X as wide as high. Head 1.2 X as wide as high; eyes densely short-haired; front moderately broad, middle interocular line 0.60 X width of head; eyes convergent above, lower interocular distance about 1.1 X upper; ocelli in a broad triangle, postocellar line 1.6 X ocello-ocular line. First four antennal segments in a ratio of about 29:10:23:27, segment three 0.51 X upper interocular distance. Front shining, very closely punctate. Pronotum rather long, its posterior margin subangulate; mesoscutum closely punctate; postnotum complete, only about a third as long as metanotum. Propodeum, in profile, sloping very weakly on the anterior two-thirds, then abruptly declivous behind; surface of propodeum covered with fine, closely parallel transverse striae. Front legs weakly incrassate; middle and hind tibiae not at all spinose; claws with the tooth strong, erect, the outer ray curved so as to be nearly parallel to it. Basal and transverse median veins of fore wing interstitial; radial vein strongly angulate at second intercubital vein; transverse median vein of hind wing strongly oblique, the submedian cell almost devoid of setulae; anal lobe small, about 0.3 as long as submedian cell.

Remarks. — This large species appears closely allied to *bifasciatus* and to *jocosus,* but there are prominent color differences as well as differences in the postnotum, shape of the propodeum, spines of the hind tibiae, and so forth. Although *innubus* belongs to this group and is known from the male only, from a locality only a few hundred miles from the type locality of *inca,* it seems much too small and differently colored to represent the male of this species.

DELICATUS SPECIES-GROUP

Epipompilus delicatus Turner

The male of this species was described by Evans, 1966, Mem. Amer. Ent. Soc., 20: 33. The genitalia are most similar to those of *pulcherrimus,* although the subgenital plate is very different and much like that of *excelsus* Bradley. As a result of other new sex associations in the genus, I feel more confident that this male is correctly associated with the female *delicatus* than I did when describing it.

I have seen one additional female of this species, collected at Turrialba, Costa Rica, by Kenneth Cooper [collection of U. S. National Museum]. This specimen is of the same size as the type and is very similar structurally, but there are some minor color differences: the greater part of the second tergite is rufous, upon which two whitish spots are imposed; tergite five also has large, paired whitish markings against a rufous background (these may be present but concealed in the type); the legs are mostly rufous but are irregularly tinged with brownish.

Epipompilus nigribasis (Banks)

This species was transferred to *Epipompilus* by Evans, 1966, Mem. Amer. Ent. Soc., 20: 31. It has been known only from the type female, from Panama, but I have recently discovered two males which unquestionably belong here. One is from Colombia: Bonda, August, Acc. no. 1999 [Acad. Nat. Sci. Philadelphia], the other from Rio de Janeiro, Brazil, 7 March 1966 (H. and M. Townes) [coll. H. K. Townes]. The small size and close coincidence of the wing venation with that of the female lead me to feel confident of this association. The eyes of the female are unusually strongly hairy, and these are the only known males having strongly hairy eyes. Although the two males are from widely separated localities, the genitalia and all other features are closely similar.

Description of male. — Length 2.5-3.5 mm; fore wing 2.2-3.0 mm. Head black; thorax and abdomen dark castaneous to fuscous, without white or rufous markings; antennae light brown, the flagellum darker on the upper surface; coxae and hind femora and tibiae dark brown, legs otherwise light to medium brown, the spurs brownish; wings subhyaline, the fore wings with a brownish cloud at the marginal and submarginal cells. Body extensively clothed with short, light brown setae; eyes densely covered with short setae.

Clypeus truncate, slightly wider than lower front. Head about 1.10 X as wide as high, the vertex forming an even arc above the eye tops; eyes strongly convergent below, lower interocular distance only 0.8 X upper interocular; middle interocular line 0.57-0.61 X width of head; ocelli in an obtuse triangle, post-ocellar line 1.2-1.6 X ocello-ocular line. Front alutaceous and with shallow punctures. Antennae rather long, the flagellum crenulate in profile; first four segments in a ratio of about 6:2:5:6, segment three 1.6 X as long as thick; flagellar pubescence coarse. Pronotum very short, arcuate behind; pro- and mesonota somewhat shining, with shallow, irregular punctures; postnotum very short, concealed medially by the overhanging metanotum; slope of propodeum low and even. Hind tibiae with some unusually long spines for the genus; claws with the tooth short, erect, except outer claws of front tarsus strongly curved, bifid. Basal vein of fore wing arising well beyond transverse median vein; marginal cell large, the radial vein angulate at second intercubital vein; hind wing with transverse median vein weakly oblique, almost perpendicular to median vein; anal lobe very small, hardly more than a minute scale with a fringe of setae (as it is in the female). Subgenital plate shaped much as in *excelsus,* but with fewer setae (Fig. 5). Genitalia with the aedoeagus exceedingly small; parapenial lobes abruptly expanded on apical half; parameres short, setose (Fig. 6).

Epipompilus tucumanus new species

Holotype. — ♀, ARGENTINA: Horco Molle, Tucuman, 25 March-30 April, 1966 (C. C. Porter) [MCZ, No. 31320].

Description of type female. — Length 8.5 mm; fore wing 7.0 mm. Head black, except antennal lobes with ivory-white spots, apical half of mandibles testaceous; pronotum black, its posterior margin with a whitish band which does not include the posterior lobes but extends broadly across the shoulders to the anterior margin, the bands irregularly bordered with rufous; mesoscutum

black except ferruginous on the midline posteriorly; remainder of thorax and propodeum entirely ferruginous; abdomen black except basal third of first tergite as well as basal 1.3 sternites ferruginous, and with the following ivory-white: large, paired spots on tergite two, large, connected spots on tergite five, and a median spot toward the base of tergite six; antennae fuscous except each of the first three segments with an ivory-white spot above; front coxae black, with a whitish spot apically, middle and hind coxae ferruginous, with black and white markings apically, middle and hind femora ferruginous except black apically, legs otherwise fuscous (including spurs) except middle and hind tibiae with whitish markings on outer surface. Fore wings strongly twice-banded, faintly luteous between bands, but apices hyaline; hind wings hyaline, the tips clouded. Body wholly clothed with short, pale pubescence.

Clypeus arcuately emarginate, measuring 2.3 X as wide as its median length. Head 1.2 X as wide as high; eyes wholly covered with short hairs; front narrow, middle interocular line 0.56 X width of head; eyes convergent below, lower interocular line 0.9 X upper; front angle of ocellar triangle slightly exceeding a right angle, postocellar line 1.2 X ocello-ocular line. First four antennal segments in a ratio of about 19:7:18:24, the third segment 0.53 X upper interocular line. Front somewhat shining, the punctures rather shallow. Pronotum arcuate behind; mesoscutum minutely, shallowly punctate; postnotum a very narrow transverse band; slope of propodeum low and even, the median line not impressed. Front femora not incrassate; hind tibiae with numerous short, dark spines; claws with the tooth strong, erect. Fore wing with the basal and transverse median veins interstitial; radial vein not at all angled at second intercubital vein; hind wing with the transverse median vein oblique, the anal lobe very small, about 0.3 the length of the submedian cell.

Allotype. — ♂, ARGENTINA: Horco Molle, Tucuman, 15-21 May 1966 (L. Stange) [Coll. H. K. Townes].

Description of allotype male. — Length 5.0 mm; fore wing 4.7 mm. Head black, except marked with whitish around antennal insertions, on extreme lower inner orbits, and on basal half of clypeus; thorax and propodeum black, with some bluish reflections, except posterior margin of pronotum white (not reaching lateral lobes); abdomen black, with bluish reflections; antennae dark brown, blackish on upper surface; palpi light brown to testaceous; front coxae black on basal third, middle section light ferruginous, apex white, middle coxae black at base but mostly light

ferruginous, hind coxae black with white tips; all trochanters fuscous; front legs beyond trochanters light ferruginous, also middle femora; middle legs beyond femora lightly infuscated, also middle spurs; hind femora, tibiae, tarsi, and spurs black, except tibiae with a basal white spot; wings hyaline, fore wings weakly infuscated on outer third. Body pubescence pale, silvery.

Clypeus arcuate emarginate, measuring twice as wide as high. Head 1.1 X as wide as high, the vertex elevated in an even arc above the eye tops; inner orbits converging below, lower interocular line only 0.7 X upper; middle interocular line 0.60 X width of head; ocelli in an obtuse triangle, postocellar line only 1.1 X ocello-ocular line. Eyes not hairy. Front alutaceous, punctate. Antennae moderately elongate, weakly crenulate in profile; first four segments in a ratio of about 13:5:9:8, segment three nearly twice as long as thick. Pronotum short, its posterior margin broadly arcuate; mesoscutum strongly punctate; median portion of postnotum nearly as long as metanotum, smooth and polished; slope of propodeum very low. Claws dentate except outer claws of front tarsi strongly curved, bifid; hind tibiae with a number of spines extending above the coarse pubescence. Wing venation not differing appreciably from that of female. Subgenital plate essentially the same as in *excelsus* (Bradley) (see Evans, 1961, Psyche, p. 34, fig. 3). Genitalia differing from those of *excelsus* in only a few details: the volsellae are considerably more slender and elongate, and the parameres are slightly broader, tapering to a subacute point on the apical third, and slightly more strongly setose.

Paratypes. — 4 ♀ ♀, same data as type [Mus. Comp. Zool., U. S. Nat. Mus., and Inst. Miguel Lillo, Tucuman]. 1 ♀, Jujuy, Argentina, 15 Jan. 1966 (H. and M. Townes) [Coll. H. K. Townes].

Additional specimen (not designated a paratype). — 1 ♀, San Esteban, near Puerto Cabello, Venezuela, 14 Jan. 1940 (P. J. Anduze) [Coll. H. K. Townes].

Variation. — The paratypes vary in length from 7.0 to 8.5 mm, fore wing from 6.0 to 7.0 mm. The third antennal segment varies from 0.45 to 0.55 X the upper interocular line, the lower interocular line from 0.85 to 0.95 X the upper. There are no differences in color or structure worthy of note.

The Venezuela specimen is similar to the type series in many respects, and it seems to me very probable that it belongs with this species. In size and all standard measurements it falls within the ranges expressed above, and the wing venation is similar, although the wings have more of a yellow tinge toward the base.

There are several color differences: the mandibles are mostly testaceous; the antennae are medium brown except the first three segments yellowish below, white above; the pronotum has a very broad ivory-white band, though occupying the same position as in the types; the front femora are brownish, the middle and hind femora fuscous, the coxae rather extensively mottled with black; the first abdominal segment is wholly black, the spots on tergite two confluent medially.

Epipompilus excelsus (Bradley)

This species is characteristic of southeastern Brazil, and appears to be relatively common for the genus. Fritz Plaumann, of Nova Teutonia, Santa Catarina, has now sent me 13 females and 33 males from that locality, collected August through April. I have also seen one female and 16 males from Rio de Janeiro, collected in March, 1966, by Henry and Marjorie Townes, as well as 10 males from Alto da Serra, Morretes, Parana, collected by the Townes in February 1966 [Coll. H. K. Townes]. I now feel convinced that the male I described in 1961 does in fact go with this species.

The series from Rio de Janeiro differs somewhat from specimens from Parana and Santa Catarina, but the male genitalia are identical and other structural differences minor. The female has a pair of white spots superimposed on the rufous base of tergite two, and the ocellar triangle is a little less broad, the postocellar line being only about 1.5 X the ocello-ocular line. The males from this locality are rather small (fore wing 3.3-4.4 mm) and also tend to have a less broad ocellar triangle; they also have somewhat more white on the legs, the front coxae having the apical 0.3-0.5 white. The genitalia of the specimens examined proved to resemble very closely the figure in my 1961 paper (p. 34, fig. 4).

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THE GENUS *NOPS* (ARANEAE, CAPONIIDAE) IN PANAMA AND THE WEST INDIES

Arthur M. Chickering

The Caponiidae include a comparatively small group of genera now known to be distributed over much of Africa, South America, Central America, southwestern part of the United States, and the West Indies. For many years I have had a continuous interest in this family and during this period I have accumulated a rather large collection of certain genera in the family. I have had a special interest in the genus *Nops* and this seems to be a convenient time to record my understanding of this genus as it is now believed to occur in Panama and the West Indies.

Again, I wish to express my appreciation and gratitude for the aid and encouragement in the pursuit of my studies extended by the staff of the Museum of Comparative Zoology for many years. My thanks are also extended to Dr. W. J. Gertsch, American Museum of Natural History, for the loan of numerous Caponiidae from Central America and the West Indies. Grants GB-1801 and GB-5013 from the National Science Foundation have made it possible for me to continue my studies in the Museum of Comparative Zoology and to spend a total of nearly eleven months collecting in Panama and the West Indies.

With the exception of the type of *Nops gertschi* sp. nov., all types named in this paper together with all other specimens belonging to the genus *Nops* in my personal collection will be deposited in the Museum of Comparative Zoology.

Genus NOPS MacLeay, 1839

Type species is *Nops guanabacoae* by monotypy.

The genus *Nops* was established on the basis of a female from Cuba. Since that time a dozen additional species have been recognized from South and Central America and the West Indies. The

most important features of the genus observed during my study of the group may be stated as follows: Carapace low; widest opposite or just behind the second coxae; considerably narrowed at anterior end; median thoracic groove or pit obscure. Eyes: two, on a slightly raised tubercle; separated by less than their diameter. Chelicerae of moderate size; with no teeth along fang groove but with a relatively large, soft lobe on the promargin (Fig. 11); fang evenly curved; with conspicuous striations on lateral surfaces. Maxillae: robust; lobate at base; strongly convergent; obtusely terminated distally and not narrowed as in *Caponina;* somewhat concave near middle. Lip: usually firmly united to sternum; about as broad as long. Sternum: with a well marked margin; raised somewhat from margin and then flat throughout; nearly oval in outline; widest opposite interval between second and third coxae. Legs: 4123 in order of length; coxae 1243 in order of length; all tarsi with three claws each but third claw often hidden; first and second tarsi with a proximal, ventral, membranous lobe; all tarsi bisegmentate; first and second metatarsi with a median, ventral, membranous fold nearly or quite throughout the segment; first and second coxae lobate at base. Palp: femur in both sexes with a small, prolateral cusp at its base in opposition to the cheliceral striations; with a more or less conspicuous, tibial brush on the prolateral side near distal end in both sexes; in both sexes the tarsus bears a dorsal, distal, oval pad of fine hairs; in females the tarsus lacks a terminal claw; in males the tarsus is simple but usually more or less distinctive. Abdomen: elongate; ovoid; with four spiracles clearly shown; six spinnerets with anterior and median pairs nearly in a transverse row; females usually with a moderately well developed scutum from genital groove to pedicel but this is usually poorly developed in males; females have no definite epigynum.

I have been obliged to transfer *Caponina blanda* Bryant to the genus *Nops* on the basis of what I regard as very clear and definite evidence. After a period of uncertainty I have also come to the conclusion that *Nops coccineus* Bryant belongs to *Nops blandus. Caponina darlingtoni* Bryant, known only from a female taken in the Dominican Republic, has been rather carefully examined with the conclusion that it probably deserves to be placed in a new genus. Its status can be determined only when males are available for study. The total list of species belonging to the genus *Nops,* as presented in this paper, may be given as follows: *Nops blandus* (Bryant); *Nops coccineus* Simon; *Nops craneae* sp. nov.; *Nops flutillus* sp. nov.; *Nops gertschi* sp. nov.; *Nops glaucus* Hasselt;

Nops guanabacoae MacLeay; *Nops largus* sp. nov.; *Nops simla* sp. nov.; *Nops toballus* sp. nov.; *Nops ursumus* sp. nov. With the exception of *Nops gertschi* sp. nov., all new species listed above are known from both sexes.

Key to male Nops *from Panama and the West Indies*

1a. Species with embolus nearly as long as or longer than the cymbium (*craneae, guanabacoae, largus, simla*) 2

1b. Species with embolus distinctly shorter than the cymbium (*blandus, coccineus, flutillus, gertschi, toballus, ursumus*) 5

2a. Species with distinct dorsal abdominal spots on a light background (*craneae, simla*) 3

2b. Species without distinct dorsal abdominal spots (*guanabacoae, largus*) 4

3a. Abdomen with a central, longitudinal, irregular, grayish stripe and and a series of four irregular, grayish spots on each side ..*craneae*, p. 6

3b. Abdomen with a series of paired purplish spots along the dorsal surface; without a central stripe .....*simla*, p. 13

4a. Embolus somewhat sinuous .....*largus*, p. 11

4b. Embolus not sinuous; somewhat swollen near middle .....
.....*guanabacoae*, p. 11

5a. Species with at least somewhat definite dorsal abdominal spots (*coccineus, gertschi, ursumus*) 6

5b. Species with no definite dorsal abdominal spots (*blandus, flutillus, toballus*) 8

6a. Abdomen with a central, dorsal, indented, brownish stripe consisting of four interconnected, irregular angular spots; each lateral side with a brownish stripe .....*coccineus*, p. 5

6b. Abdomen lacking such a color pattern as given above (*gertschi, ursumus*) 7

7a. Abdomen with a series of five pairs of dark grayish, dorsal spots .....*ursumus*, p. 16

7b. Abdomen grayish in general, with two light greenish bars in anterior two-thirds; without any such distinct series of spots as given above .....*gertschi*, p. 9

8a. Embolus short; about half as long as tarsal bulb .....*blandus*, p. 4

8b. Embolus longer; nearly or quite as long as tarsal bulb (*flutillus, toballus*) 9

9a. Abdomen purplish dorsally .....*flutillus*, p. 7

9b. Abdomen gray dorsally .....*toballus*, p. 14

Except for the females with a distinct abdominal color pattern this sex is conspicuously lacking in characters with can be used in constructing a key for their separation into species. For this reason no satisfactory key for their separation has yet been devised.

Nops blandus (Bryant)
Figures 1–2

Caponina blanda Bryant, 1942: 328, pl. 2, fig. 17. The male holotype from St. Croix, U. S. Virgin Islands, is in the Museum of Comparative Zoology.

Nops coccineus, — Bryant, 1948: 344. (Not *Nops coccineus* Simon.)

Caponina blanda Bryant must be transferred to *Nops* because it very clearly exhibits the characters of the latter genus. Until recently I have considered the specimens called *Nops coccineus* by Miss Bryant, from Haiti, as a new species and intended to describe it as new. Recently, however, following careful comparison with *N. blandus,* I have been forced to place them together. There are minor differences but, in my judgment, no greater than are commonly found among individuals of the same species (Figs. 1-2).

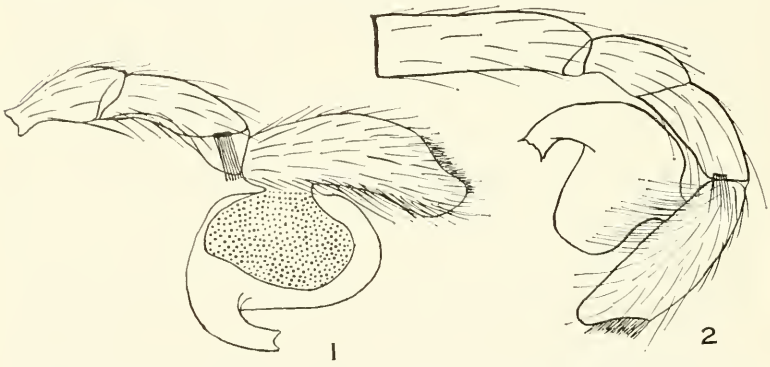


Figure 1. *Nops blandus* (Bryant). Left male palp; prolateral view. Fig. 2. *Nops coccineus* Bryant (= *Nops blandus* (Bryant)). Left male palp; prolateral view.

I had hoped to collect specimens of *Nops blandus* during my two recent visits to St. Croix but I failed to find any members of the genus. I now have two males from St. John together with several immature specimens collected in July, 1966; I also have a female together with two immature specimens collected in February, 1964. These are all tentatively placed in *Nops blandus* pending more data on the *Nops* population of these islands. During my recent visit to Virgin Gorda, British Virgin Islands, I collected two mature males, one female, and two immature specimens. These were all taken on August 18, 1966, and are also tentatively placed in this species.

A female *Nops* and several immature specimens collected on St. Thomas in February, 1964, and in July, 1966, are not yet definitely assigned to species.

Nops coccineus Simon

Figure 3

Nops coccineus Simon, 1891, fig. 18, pl. 42. Male and female syntypes from St. Vincent, B. W. I., are in the British Museum (Natural History). Simon, 1893: 324; Petrunkevitch, 1911: 133; Lutz, 1915: 82; Berland, 1932: 339; Roewer, 1942: 316; Bonnet, 1958: 3114.

While working in the British Museum in the summer of 1958, I had an opportunity to examine both sexes of *Nops coccineus* Simon. The following notes were written during my examination of these specimens. Female: length from anterior border of clypeus to posterior end of anal tubercle 8.78 mm; carapace 2.99 mm long; 2.26 mm wide opposite interval between second and third coxae where it is widest; regularly rounded posteriorly but much narrowed in front; about 1.3 mm tall. Two eyes circular and separated by a little more than the radius of one. Height of porrect clypeus 3.25 times the diameter of an eye. Chelicerae with a fleshly lobe just promarginal to fang; no teeth observed; markedly striate along

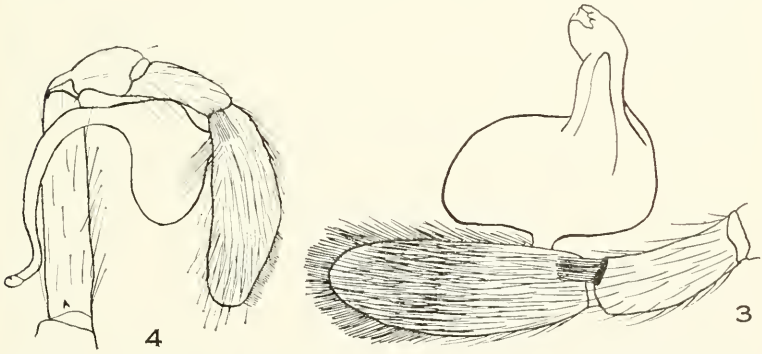


Figure 3. *Nops coccineus* Simon. Left male palp; prolateral view. Fig. 4. *Nops craneae* sp. nov. Left male palp; prolateral view.

outer surfaces; opposing palpal, femoral cusps moderately developed. Tarsi 1 and 2 with a small third claw; tarsi 3 and 4 with a somewhat more prominent third claw; all tarsi bisegmentate; tarsi 1 and 2 with the usual ventral, proximal lobe. Metatarsi 1 and 2

with the usual ventral, median, longitudinal, membranous fold. Sternum only extended to bases of fourth coxae. Epigynal area lightly cornified. Color in alcohol: cephalothorax very reddish; legs somewhat lighter; abdomen yellowish dorsally with a central, indented, brownish stripe consisting of four connected, irregularly angular spots. Male: essential features of the male palp shown in Figure 3; total length from anterior border of porrect clypeus to posterior end of posterior spinnerets 5.6 mm; color in general like that of female but clearer; each lateral side of abdomen with a brownish stripe, very irregular; venter yellowish.

Nops craneae sp. nov.

Figure 4

Holotype. The male is from Simla, Arima Valley, Trinidad, W. I., in the close vicinity of the Wm. Beebe Tropical Research Station, April 17, 1964. This species is named after Miss Jocelyn Crane, director of the station.

Description. Total length from anterior border of clypeus to posterior end of extended spinnerets 7.8 mm; length from anterior border of clypeus to posterior end of abdomen 7.21 mm. Carapace 3.25 mm long; 2.34 mm wide opposite interval between second and third legs where it is widest; only about 0.55 mm tall; only a slight indication of a median, thoracic fovea; surface very finely granulate. Eyes: two as usual on a slightly raised tubercle; separated from one another by slightly less than the radius of one; height of clypeus equal to nearly 2.75 times the diameter of an eye. Chelicerae, maxillae, lip and sternum essentially as given in statement of characters of the genus. Legs: tibial index of first leg 13, of fourth leg 9; no spines observed on legs; typical of the genus in regard to tarsal bisegmentation, tarsal claws, tarsal basal, ventral lobes and metatarsal ventral, longitudinal folds. Palp: essential features shown in Figure 4; cusp at base of femur on prolateral surface; oval, dorsal, tarsal pad of short, fine hairs as usual; all segments simple except the tarsus. Abdomen: typical of the genus. Color in alcohol: carapace and sternum a dark reddish; considerable black pigment in ocular area; legs and mouth parts reddish brown in general but with variations; metatarsi 1 and 2 and the proximal divisions of tarsi 1 and 2 very light yellowish. Abdomen: light greenish with dark gray spots; an irregular, median, dark gray stripe extends throughout the dorsum; on each dorsolateral side there is a series of 4 irregularly elongated, dark gray spots the last of which spreads and unites with the median stripe; the venter has

two small and very irregular, dark gray spots and a pair of larger gray spots in a ventrolateral position; the greenish coloration is somewhat darker in the region of the tracheal spiracles.

Female paratype. The described female paratype measures 10.34 mm from anterior border of clypeus to posterior end of abdomen; from anterior border of clypeus to posterior end of spinnerets 11.25 mm. Carapace 4.03 mm long; 3.06 mm wide opposite second coxae where it is widest; otherwise essentially as in male holotype. Eyes: two, separated by about ⅝ of their diameter; height of clypeus equal to about 3.5 times the diameter of an eye. Chelicerae, maxillae, lip and sternum essentially as in male. Legs: tibial index of first leg 14, of fourth leg 10; tarsal claws, tarsal, basal, ventral lobes, metatarsal ventral, membranous folds and other features as stated for the genus all typical. Abdomen: essentially as in male; scutum only moderately developed anterior to genital groove. Color in alcohol: nearly identical to that of male; abdominal color pattern clear and definite; venter with three very irregular, dark spots on each ventrolateral side; the first of these is lateral to the scutum, the second is a little behind the middle and somewhat nearer the middle line, while the third is anterior to the spinnerets and still nearer the middle line.

Records. The described female paratype is also from Trinidad, W. I., with no date of collection (N. A. Weber). Two females are in the collection with the described female paratype; two immature specimens from Balandra Bay, Trinidad, April, 1922 (Reynolds collection). I took eight specimens in April, 1964, in the vicinity of Simla, Arima Valley, Trinidad, W. I. One immature specimen from Piarco (A. M. Nadler), January, 1955, and a female from Gasparee, November, 1944 (T. S. Jones) are tentatively placed here.

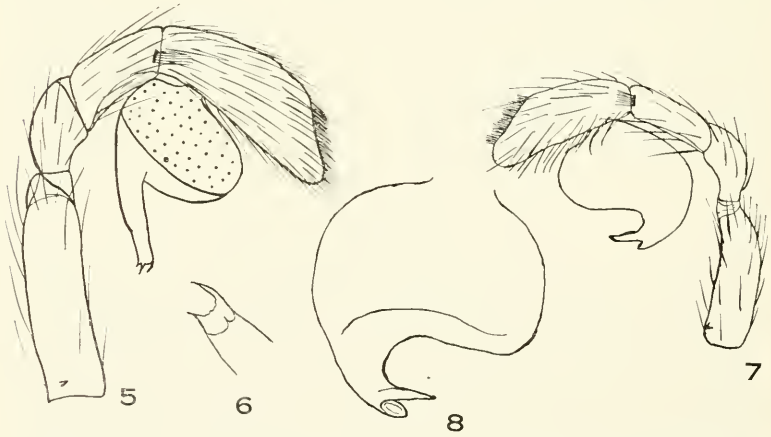
NOPS FLUTILLUS sp. nov.

Figures 5-6

Holotype. The male holotype and described female paratype are from the Dutch West Indies, Curaçao, Sint-Nicolaas; St. Marthaa, December 29, 1962 (B. de Jong and H. W. Levi).

The specimens referred to this species were tentatively placed under the name *Nops glaucus* Hasselt — a species based upon a female from the West Indian island of Bonaire. After a period of some uncertainty the decision has been made to regard the species as new. The name of the species is an arbitrary combination of letters.

Description. Total length of male from anterior border of clypeus to posterior end of abdomen 5.79 mm. Carapace 2.5 mm long; 1.87 mm wide opposite second coxae where it is widest; about 0.55 mm tall; otherwise essentially typical of males of the genus. Eyes: two as usual; separated by about $^{3}/_{14}$ of their diameter. Chelicerae, maxillae and lip essentially typical of males of the genus. Sternum: longer than wide in ratio of about 6 : 5; somewhat more oval in outline than usual; fourth coxae separated by about $^{3}/_{10}$ of their width; otherwise quite typical of the genus. Legs: tibial index of first leg 14, of fourth leg 10; tarsi typical with respect to bisegmentation, claws, and ventral, proximal, membranous lobes; metatarsi also typical with respect to the ventral, medial, membranous fold; no spines but with many hairs and bristles; trichobothria observed on tarsi, metatarsi, tibiae and, possibly, also on palpal segments. Palp: essential features shown in Figures 5-6. Abdomen apparently typical of the genus in all essential features. Color in alcohol: all parts except abdomen essentially as described for *N. largus* sp. nov.; abdomen purplish over most of the dorsum, becoming darker and broader posteriorly; lateral sides yellowish, becoming purplish posteriorly; venter with a fairly well defined scutum anterior to genital groove and with light green color around a broad margin; remainder of venter yellowish with purplish dots, becoming more definitely purplish toward posterior end.



Figures 5-6. *Nops flutillus* sp. nov. Fig. 5. Left male palp; prolateral view. Fig. 6. Tip of embolus, more enlarged; retrolateral view. Figs. 7-8. *Nops gertschi* sp. nov. Fig. 7. Right male palp; prolateral view, Fig. 8. Tarsal bulb, more enlarged; retrolateral view.

Female paratype. The described female paratype has a total length of 8.45 mm from anterior border of porrect clypeus to posterior end of abdomen. Carapace 4.03 mm long; 3.04 mm wide opposite posterior border of second coxae where it is widest; 0.96 mm tall; otherwise essentially typical of the genus. Eyes: two as usual on a low tubercle; separated by nearly ¾ of the diameter of an eye; height of porrect clypeus equal to about 4.5 times the diameter of an eye. Chelicerae, maxillae, lip and sternum all essentially typical of females of the genus. Legs: tibial index of first leg 18, of fourth leg 13; tarsi typical with respect to claws, bisegmentation, and basal, ventral lobes; metatarsi typical with respect to ventral, medial, longitudinal folds; claw tufts moderately developed; with no palpal tarsal claws; with the usual, distal, prolateral, tibial, palpal brush. Abdomen: essentially as in male; a well defined scutum occupies the whole area of tracheal spiracles continued to the pedicel; what has frequently been termed the epigynum is a slightly recurved slit between anterior spiracles. Color in alcohol: essentially as in male holotype with minor variations; with considerable light green color in parts of the ventral scutum.

Records. One male paratype, two female paratypes and two immature specimens taken with the holotype. One male paratype and eleven immature specimens from several localities on the island of Curaçao collcted by Dr. and Mrs. H. W. Levi and Mr. B. de Jong in December, 1962.

NOPS GERTSCHI sp. nov.

Figures 7-8

Holotype. The male holotype is from Loma Cibao, La Vega, Dominican Republic, August 9, 1956, 600-1600 m elevation (Dr. Allan F. Archer, E. B. M.). The holotype will be deposited in the American Museum of Natural History, New York, N. Y.

Until recently the specimen described here as a new species was regarded as another specimen of *Nops blandus* (Bryant) but study has convinced me that it must be regarded as new. The species is named after Dr. W. J. Gertsch.

Description. Total length from anterior border of clypeus to posterior end of abdomen 5.98 mm; from tip of somewhat porrect chelicerae to posterior end of abdomen 6.18 mm. Carapace 2.86 mm long; 2.08 mm wide opposite second coxae where it is widest; narrowed to about 0.78 mm at anterior end. Eyes: two as usual on a low tubercle; separated by their diameter; surrounded

by black pigment, lighter between the eyes; height of porrect clypeus equal to nearly 3.75 times the diameter of an eye. Chelicerae, maxillae, lip and sternum all essentially typical of males of the genus; fourth coxae separated by their width. Legs: tibial index of first leg 14, of fourth leg 9; tarsi typical as stated in description of the genus; metatarsi 1 and 2 also typical with respect to the ventral, longitudinal, membranous fold; typical with respect to other observed features. Palp: essential features shown in Figures 7-8; palpal, tibial, prolateral brush apparently lacking on left palp. Abdomen: essentially typical of males of the genus. Color in alcohol: carapace and sternum an orange yellow; with considerable black pigment in ocular area; legs nearly the same as carapace dorsally but lighter ventrally; lip and chelicerae like sternum; maxillae lighter; palp like legs with variations. Abdomen: dorsum grayish in general but with two irregular, light greenish, dorsolateral bars in anterior two-thirds; lateral sides dark grayish with ventral extensions of the lighter dorsal, irregular bars; venter yellowish with a faint greenish tint anterior to genital groove; posterior to genital groove light greenish with irregular dark spots for nearly three-quarters of the distance to the spinnerets; the area immediately in front of the spinnerets is dark like most of the dorsum.

Nops glaucus Hasselt

Nops glaucus Hasselt, 1887: 77, figs. 1-4, 10. Female holotype from Bonaire, Dutch West Indies, in the Natural History Museum, Leiden. Simon, 1892: 449; Petrunkevitch, 1911: 134; Roewer, 1942: 316; Bonnet, 1958: 3114.

Through the courtesy of Dr. van der Hammen of the Natural History Museum in Leiden I have been able to examine the holotype of this species from which I have derived the following: total length 9.17 mm from anterior border of clypeus to posterior end of abdomen; carapace 3.9 mm long and 2.92 mm wide opposite interval between second and third legs. Eyes: two as usual on a low tubercle; separated by nearly three-fourths of the diameter of an eye; height of clypeus nearly equal to four times the diameter of an eye. Legs: typical of the genus in all respects as given in the description of the genus. The usual palpal, tibial brush is present. The color appears to have faded somewhat during long preservation. Legs and palps light yellowish; carapace, sternum, and other mouth parts all reddish brown; abdomen light grayish with a purplish tint dorsally and yellowish ventrally. I consider the original drawings very good with one exception; in figure 1 the second femur

is over-inflated; in the holotype under observation the second femur is only normally robust. Simon reported this species from Venezuela in 1892. Apparently it has not been definitely recorded since that time.

Nops guanabacoae MacLeay
Figures 9-10

Nops guanabacoae MacLeay, 1839: 1-14, pls. 1-2. The female holotype from Cuba is probably in the British Museum (Natural History), London. Walckenaer, 1842: 442; Hasselt, 1887: 71; Simon, 1893: 328; Petrunkevitch, 1911: 133; Bryant, 1940: 271; Roewer, 1942: 316; Bonnet, 1958: 3114.

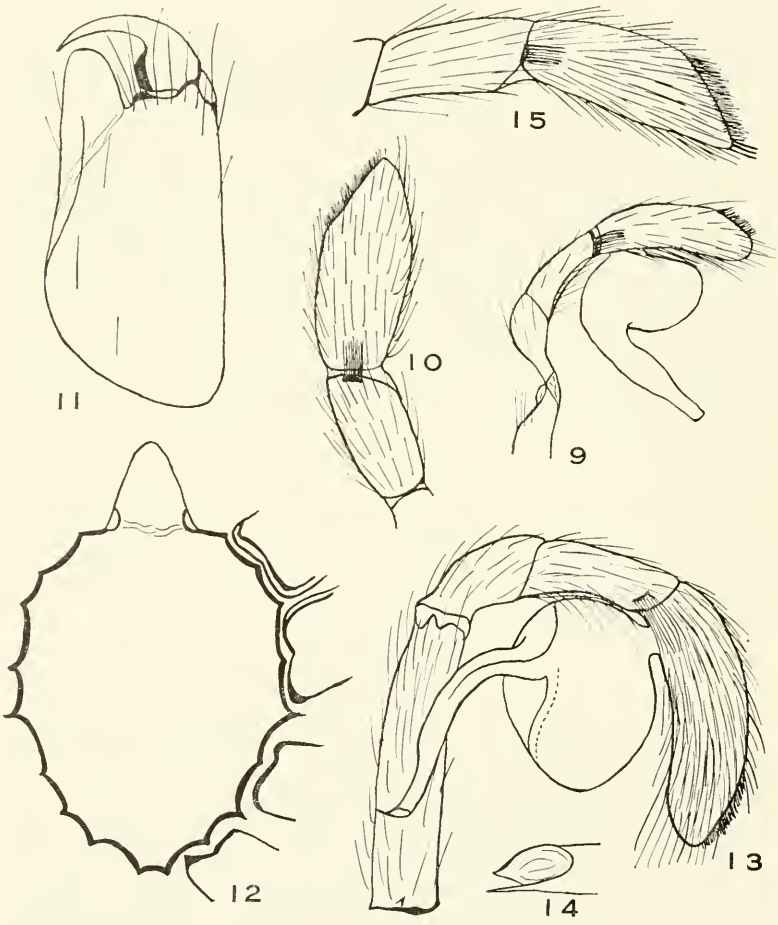
The male was unknown until 1940 when Miss Bryant described it and had both sexes for study. As a result of my examination of these specimens I am obliged to disagree with several of the published statements concerning the male. These may be briefly stated as follows: eyes separated from one another by nearly ⅗ of the diameter of one of them; chelicerae with the usual fleshy lobe on the promargin of the fang groove; lip firmly united to sternum and only a little longer than wide; legs 4123 in order of length; all tarsi with three claws; tarsi 1 and 2 with the typical ventral, proximal lobe; metatarsi 1 and 2 with the ventral, median, membranous fold; the usual palpal, tibial brush is present in both sexes. Essential features of the male and female palps are shown in Figures 9-10. There are now two mature males together with several females and immature specimens from several localities in Cuba, and the species is, apparently, known only from that island.

Nops largus sp. nov.
Figures 11-15

Holotype. The male is from the Panama Canal Zone Forest Preserve, January 21, 1958. The name of the species is a Latin adjective referring to its abundance in its natural habitat.

Description. Total length 6.7 mm from anterior border of clypeus to posterior end of abdomen; from anterior border of slightly extended chelicerae to posterior end of spinnerets 6.89 mm. Carapace 3.15 mm long; 2.34 mm wide opposite second coxeae where it is widest; about 0.7 mm tall. Eyes: two as usual on a slightly raised tubercle; separated by slightly less than their radius; height of porrect clypeus nearly equal to 2.66 times the diameter of an eye. Chelicerae, maxillae and lip essentially

typical of the genus; cheliceral fleshy lobe shown in Figure 11. Sternum: surface rather coarsely granulate; coxae 1 and 2 basally lobed as usual; terminated just posterior to bases of fourth coxae which are separated by about their width (Fig. 12). Legs: tibial index of first leg 14, of fourth leg 11; spines lacking; tarsal claws, ventral, proximal lobes on tarsi 1 and 2 and ventral, medial,



Figures 9-10. *Nops guanabacoae* Macleay. Fig. 9. Left male palp; prolateral view. Fig. 10. Left female palp; prolateral view. Figs. 11-15. *Nops largus* sp. nov. Fig. 11. Left chelicera of male. Fig. 12. Sternum of male. Fig. 13. Left male palp; prolateral view. Fig. 14. Tip of embolus; enlarged. Fig. 15. Left female palp; prolateral view.

longitudinal folds on metatarsi 1 and 2 all typical of the genus. Palp: essential features shown in Figures 13-14. Abdomen: quite typical of the genus; ventral scutum rather poorly developed; with a copious supply of short hair. Color in alcohol: carapace and sternum a bright orange red; legs generally somewhat lighter dorsally and still lighter ventrally; all coxae and mouth parts yellowish with variations. Abdomen: greenish gray with many narrow, light colored lines running in a variety of directions; lateral sides grayish with the gray areas extending to ventral surface and covering the posterior fourth of the venter with the remainder nearly white with greenish spots around spiracles. Considerable variation in coloration has been noted among paratypes with a tendency for a purplish color to replace the greenish gray.

Female paratype. Total length of described female paratype 8.58 mm from anterior border of clypeus to posterior end of abdomen; from anterior border of slightly porrect chelicerae to posterior end of spinnerets 8.78 mm. Carapace 3.84 mm long; 2.86 mm wide opposite second coxae where it is widest; 0.58 mm tall; posterior end transversely rugulose; with a series of light colored, fine, intricately branched lines covering entire surface; otherwise as in male. Eyes: two as usual; separated by about ⅔ of their diameter; height of porrect clypeus equal to about 3.3 times the diameter of an eye. Chelicerae, maxillae, lip and sternum essentially as in male and typical of females of the genus. Legs: tibial index of first leg 15, of fourth leg 9; essentially as in male with respect to the ventral lobe on tarsi 1 and 2, the median, ventral fold on metatarsi 1 and 2, and tarsal claws. The palp lacks a tarsal claw but has the usual tibial brush and the femoral, prolateral, basal cusp. Abdomen: essentially as in male. Color in alcohol: essentially as in male with minor variations.

Records. The described female paratype is from Barro Colorado Island, Panama Canal Zone, January, 1958. About forty mature males together with many females and immature specimens assigned to this species have been taken in several localities in the Canal Zone and in Panama proper in El Valle, El Volcan, and Arraijan. I have found it especially abundant on Barro Colorado Island, Canal Zone.

NOPS SIMLA sp. nov.

Figures 16-17

Holotype. The male is from Simla, Arima Valley, Trinidad, W. I., in the close vicinity of the Wm. Beebe Tropical Research Station, March 31, 1964. The name of the species is a noun used in apposition after the locality where the holotype was collected.

Description. Total length 4.94 mm. Carapace 1.95 mm long; 1.45 mm wide opposite second coxae where it is widest; 0.44 mm tall; median thoracic fovea barely indicated. Eyes: two as usual; separated by about $\frac{5}{11}$ of their diameter; with a moderate amount of black pigment around eyes; height of porrect clypeus nearly equal to $2\frac{2}{3}$ times the diameter of an eye. Chelicerae, maxillae and lip with only minor variations from the typical. Sternum: very granulate; obtusely terminated between bases of fourth coxae which are separated by about $\frac{1}{5}$ of their width. Legs: tibial index of first leg 14, of fourth leg 10; tarsi typical of the genus with respect to bisegmentation and claws; tarsi 1 and 2 typical with respect to ventral, basal lobe; metatarsi 1 and 2 essentially typical with respect to ventral, medial, longitudinal fold except that this seems to be somewhat reduced in prominence. Palp: essential features shown in Figure 16; embolus very long. Abdomen essentially typical of the genus. Color in alcohol: carapace, lip and sternum a medium reddish brown; palp and other mouth parts yellowish with variations; all coxae light yellowish; other segments of legs reddish brown with variations; legs 1 and 2 somewhat the darkest. Abdomen: background color light yellowish; dorsum with a series of five pairs of light, irregular, purplish spots (Fig. 17); at posterior end there is a pair of elongated, lateral, purplish spots extending forward from the spinnerets; venter generally yellowish.

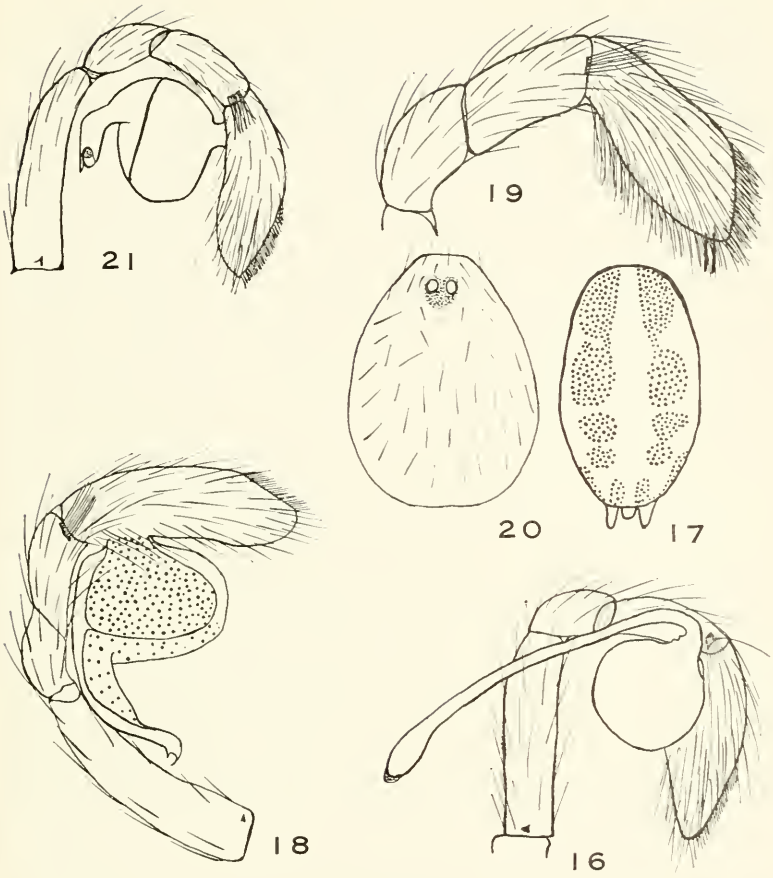
Female paratype. Total length 5.92 mm. Carapace 2.15 mm long; 1.69 mm wide opposite posterior border of second coxae where it is widest; about 0.44 mm tall. Eyes essentially as in male. Chelicerae, maxillae, lip and sternum essentially as in male. Legs: tibial index of first leg 16, of fourth leg 10; other features of legs essentially as in male and typical of the genus. Abdominal features and color essentially as in male.

Records. The female paratype was taken in the same locality as the holotype on April 25, 1964, together with an immature specimen. The following have been on loan from Dr. W. J. Gertsch: two males from Arima, Trinidad, May, 1953 (N. L. H. Kraus) and an immature specimen from Piarco, Trinidad, January, 1955 (A. M. Nadler).

Nops toballus sp. nov.

Figures 18-19

Holotype. The male holotype is from St. Catherine Parish, near May Pen, Jamaica, W. I., November 22, 1957. The name of the species is an arbitrary combination of letters.



Figures 16-17. *Nops simla* sp. nov. Fig. 16. Left male palp; prolateral view. Fig. 17. Abdomen; dorsal view. Figs. 18-19. *Nops toballus* sp. nov. Fig. 18. Left male palp; prolateral view. Fig. 19. Left female palp; prolateral view. Figs. 20-21. *Nops ursumus* sp. nov. Fig. 20. Male carapace; dorsal view. Fig. 21. Left male palp; prolateral view.

Description. Total length 3.94 mm. Carapace 1.87 mm long; 1.47 mm wide opposite second coxae where it is widest; 0.51 mm tall; surface very finely granulate; with no definite thoracic fovea. Eyes: two as usual, separated by about their radius; height of porrect clypeus equal to a little less than three times the diameter of an eye. Chelicerae, maxillae, lip and sternum essentially typical of

the genus with minor differences; fourth coxae separated by slightly more than their width. Legs: tibial index of first leg 15, of fourth leg 10; with very slender spines, hardly more than robust bristles; tarsal claws, tarsal ventral lobes and metatarsal, ventral folds on legs 1 and 2 typical of the genus. Palp: essential features shown in Figure 18. Abdomen: ovoid; with many short hairs; surface very granular; otherwise quite typical of the genus. Color in alcohol: carapace a bright orange with eyes on a black spot divided in front; legs nearly the same color above but lighter below; sternum somewhat lighter than carapace; abdomen with dorsum and lateral sides gray, venter nearly white anterior to genital groove, greenish from genital groove to near spinnerets where it becomes grayish.

Female paratype. Total length 6.18 mm, exclusive of somewhat extended posterior spinnerets; 6.5 mm long to tip of posterior spinnerets. Carapace: 2.73 mm long; 2.02 mm wide opposite second coxae where it is widest; about 0.65 mm tall; otherwise essentially as in male. Eyes, chelicerae, maxillae, lip and sternum essentially as in male with minor differences. Legs: tibial index of first leg 16, of fourth leg 10; essentially typical of the genus in respect to other features. Abdomen also essentially typical of the genus.

Records. The described female paratype is from Clarendon Parish, 3 miles north of May Pen, Jamaica, W. I., November 10, 1963. Additional specimens are in the collection from Jamaica as follows: a female from Blue Mts., Main Range, August, 1934 (P. J. Darlington, Jr.); a male from St. Thomas Parish, Morant Bay, May, 1956 (C. C. Hoff); several immature specimens from St. Andrew, St. Catherine, and St. Thomas parishes taken in 1956, 1957 and 1963.

Nops ursumus sp. nov.

Figures 20-21

Nops maculata, — Banks, 1929: 53-96, 4 pls. (Not *N. maculata* Simon).

Holotype. The male holotype was taken in a Berlese funnel on Barro Colorado Island, Panama Canal Zone, between April and June, 1950, by Dr. James Zetek. The name of the species is an arbitrary combination of letters.

Description. Total length from anterior border of clypeus to posterior end of abdomen 4.94 mm; from anterior border of clypeus to posterior end of spinnerets 5.14 mm. Carapace 2.07 mm long; 1.52 mm wide opposite posterior border of second coxae where it is widest; 0.59 mm tall; with no discernible thoracic

fovea; surface finely granulate; with a sparse covering of hair (Fig. 20). Eyes: two as usual; separated by about $\frac{1}{3}$ of their diameter; height of porrect clypeus about equal to 2.5 times the diameter of an eye. Chelicerae, maxillae, lip and sternum apparently quite typical of the genus as observed in this study. Legs: tibial index of first leg 13, of fourth leg 8; legs 1-3 only slightly different in length; typical of the genus with respect to tarsal claws, ventral, proximal lobes on tarsi 1 and 2 and ventral, median fold on metatarsi 1 and 2. Palp: essential features shown in Figure 21. Abdomen: all features essentially typical of the genus. Color in alcohol: carapace and sternum a rich, dark orange with a moderate amount of black pigment in ocular region. Mouth parts and legs reddish brown with variations. Abdomen: background color of dorsum a light greenish with five pairs of dark grayish spots; the first pair of spots are broad and extend posteriorly for a considerable distance and are separated by a narrow, greenish stripe in the middle; the remaining four pairs of spots are diagonal bars reaching forward and then downward for a very short distance ventrolaterally; the last two pairs are somewhat united and the fourth pair is considerably extended posteriorly; shortly anterior to the anal tubercle there is a single, small, irregular spot somewhat united to the most posterior pair of bars; the venter is whitish with a greenish tint; a short distance anterior to the spinnerets there is a short, median line of irregular gray dots and lateral to these is an irregular dotted area on each side.

Female paratype. Total length from anterior border of clypeus to posterior end of abdomen 9.42 mm; length from anterior border of clypeus to posterior end of spinnerets 9.94 mm. Carapace 3.45 mm long; 2.67 mm wide; 0.85 mm tall; otherwise essentially typical of females of the genus. Eyes: two as usual; separated by about their radius; height of clypeus nearly equal to 3.5 times the diameter of an eye. Chelicerae, maxillae, lip and sternum essentially typical of females of the genus; sternal suture line unusually clear but probably does not indicate freedom of movement for the lip. Legs: tibial index of first leg 12, of fourth leg 9; tarsal claws, ventral, proximal lobe on tarsi 1 and 2 and ventral, median fold on metatarsi 1 and 2 all typical of the genus. Abdomen: essentially typical of females of the genus; region from genital groove to pedicel rather poorly supplied with a scutum. Color in alcohol: essentially as in male with minor variations; here the two posterior, dorsal, abdominal bars are united to one irregularly shaped spot; the venter has scattered dark spots, the largest of which occur as a

pair of very irregular spots shortly anterior to the spinnerets.

Records. The described female paratype was taken in the same locality as the holotype, January, 1958. One mature male paratype was taken with the holotype; another male was taken by Dr. Zetek in the same locality and by the same method, Oct.-Dec., 1941. A very few females which may be mature and nearly three dozen others in various stages of immaturity are in the collection from Barro Colorado Id., C. Z. Forest Preserve, Summit Gardens, and Pedro Miguel, all in the Canal Zone. The immature specimen reported by Banks (1929) as *N. maculata* Simon quite clearly belongs in *N. ursumus* sp. nov. The following have been on loan from Dr. W. J. Gertsch: a male and a female from Barro Colorado Id., Dec. 1937-Jan. 1938 (F. J. Ryan); three immature specimens from the same locality taken July, 1930, and July-August, 1938; an immature specimen taken in Santa Rosa, Colon Prov., Panama, Sept., 1945 (C. D. Michener).

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BREVIORA

Museum of Comparative Zoology

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A NEW SCINCID LIZARD FROM THE NORTHERN SOLOMON ISLANDS

Allen E. Greer and Fred Parker[1]

During a term of duty by Parker (1962-1963) and a subsequent (1966) collecting trip by him to Bougainville and neighboring islands in the extreme northern Solomon Islands, a previously undescribed species of skink was discovered on Bougainville and Shortland Islands. A single specimen of the new species from Choiseul is also known but has previously been reported in the literature as *Sphenomorphus solomonis* (Burt and Burt, 1932:544).

On the basis of current, but not necessarily phylogenetically correct, generic concepts, the new species is assigned to the genus *Sphenomorphus* and may be known as

SPHENOMORPHUS TANNERI[2] new species

Holotype: Museum of Comparative Zoology 76551; collected by Fred Parker at Kunua, Bougainville, on 8 June 1963.

Paratypes (423 specimens): NORTHERN BOUGAINVILLE: KUNUA (100 feet above sea level): MCZ 76483, 76484, 22.vi, 11.vii.1962; MCZ 76486-76487, 25-30.xii.1962; MCZ 76488-76550, 76552-76623, 77308-77361, 78091, 78299, 84140, + 2 untagged specimens, 12.v-29.vii.1963; MELILUP (*ca.* 3000 feet a.s.l.): MCZ 89593, 92295, 92326-92339, 92366-92368, 12-20.v.1966; MUTAHI (2700 ± 500 feet a.s.l.): MCZ 87570-87577, 88799, 89102-89126, 89594, 91430-91437, 92203-92228, 92269-92294, 92296-92302, 92304-92325, 92340-92365, 92372-92377, 9-20.v.1966; RAMAZON RIVER (1600-2400 feet a.s.l.):

[1] Department of District Administration, Kundiawa, Territory of New Guinea.

[2] The new species is named for Charles Tanner, Honorary Curator of Reptiles at the National Museum, Melbourne, who introduced one of us (Parker) to reptiles several years ago and has since helped in many ways.

MCZ 92229-92236, 19.v.1966; TOPANAS (500 feet a.s.l.): MCZ 88443-88453, 8.v.1966.

SOUTHERN BOUGAINVILLE: MATSIOGU (2100 feet a.s.l.): MCZ 92379-92382, 92522, 2.iv, 24.iii.1966; PAMAUITA (1200 feet a.s.l.): MCZ 92521, 92523, 23.ii, 2.iv.1966; TURIBOIRU (260 feet a.s.l.); MCZ 87578-87580, 87727-87732, 92496-92501, 92520, 92990-92992, 9-21.iii.1966; MCZ 92369-92371, 26-27.iv.1966.

SHORTLAND: KOLIAI (10 feet a.s.l.): MCZ 89736, 11.iv.1966.

CHOISEUL: American Museum of Natural History 44004.

Diagnosis: S. tanneri differs from all other species with 28-32 midbody scales in its species group (Table 4) in the following combination of characters: small size (snout-vent length 52 mm or less); prefrontals forming a median suture; adpressed limbs widely separated; no symmetrical pairs of nuchal scales; middorsal scales subequal rather than with the scales of the two vertebral rows transversely enlarged; dorsum rich dark brown to brownish black with small paler spots on body which often coalesce on the anterior dorsolateral line to form a distinct light line.

S. tanneri is most similar in squamation to *S. nigriventre* de Rooij (1915: 214-215) from southern New Guinea, and *S. antoniorum* Smith (1927: 216-217) from Timor. It differs from *S. nigriventre* in being much smaller in size (snout-vent length 90 mm for *nigriventre*) and lacking the dorsal transverse series of light, dark-edged spots of this species. It differs from *S. antoniorum* in having the prefrontals meeting medially (prefrontals separated or just touching one another in *antoniorum*), and in lacking the light brown dorsum with a heavy clustering of darker brownish spots along the dorsolateral line.

Description (Fig. 1): A cryptic skink ranging in snout-vent length from 23-52 mm; tail slightly longer than snout-vent length; head obtusely conical; limbs pentadactyl, failing to meet when adpressed to body.

Rostral slightly wider than deep, projecting well onto dorsal surface of snout; external naris placed well forward and ventral in a single large nasal; supranasals lacking; frontonasal wider than long, forming a short suture with rostral but separated from frontal by prefrontals, i.e., prefrontals paired and meeting medially (except in one individual); single anterior and posterior loreals; frontal about as long as frontoparietals and interparietal measured along midline, obtusely rounded posteriorly and in contact with

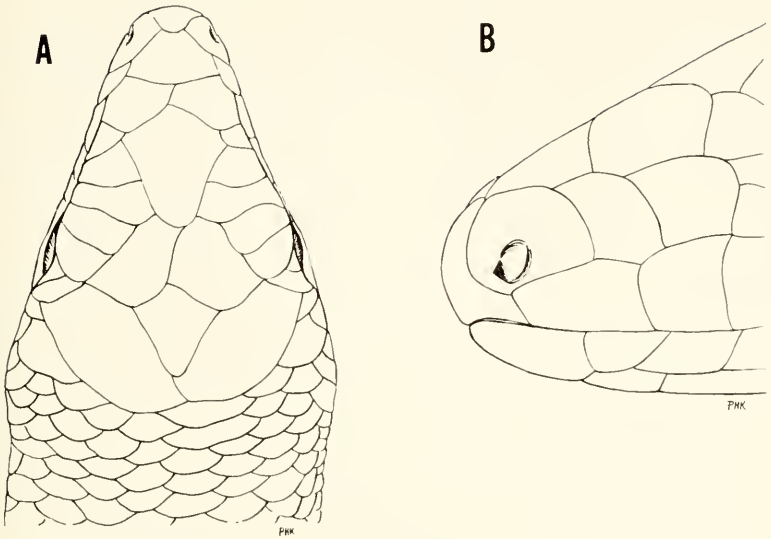

Figure 1. *Sphenomorphus tanneri* (MCZ 92304, paratype): (A) Dorsal view of the head and nape, showing two successive "nuchal" scales on the right side of the nape; (B) nasal area on the left side of the head, showing the external naris situated anteroventrally in the large nasal scale.

2 anteriormost supraoculars; 4 supraoculars; lower eyelid scaly, scales of eyelid separated from supralabials by a complete row of subocular scales; frontoparietals and interparietal distinct, approximately subequal in size; parietals meet behind interparietal; no distinct, symmetrical series of nuchals; 6-7 supralabials, 4th or 5th supralabial below center of eye (Table 1).

Ear opening oval, tympanum slightly sunk below surface; auricular lobes lacking; midbody scales smooth, in 28-32 (usually 30-32, see Table 1) longitudinal rows; midbody scales of dorsum subequal in size; a pair of enlarged preanals; 3 median rows of subcaudal scales subequal in size; 13-20 (usually 15-19, see Table 1) obtusely keeled lamellae beneath 4th (longest) toe; dorsal surface of 4th toe covered distally by a few single scales, medially by 3 longitudinal rows of scales and proximally by 4 or 5 rows (Group IV of Brongersma, 1942).

Color (Fig. 3): In life the color pattern is relatively constant. The dorsum is a rich dark brown to brownish black with small paler spots on the body and tail. Larger light spots on the anterior

dorsolateral line often coalesce to form a noticeably distinct line. The flanks are marked as the dorsum but usually lighter. The chin and throat are heavily marked with black to brown; the anterior venter is whitish to yellowish; the posterior venter and ventral surface of the tail are occasionally translucent yellow, but more often, translucent dull reddish. Some specimens have dark spots under the tail and others show a bar of fine spots on the posterior part of the throat. Preserved specimens lose the yellowish and reddish colors.

Some individuals from the southern Bougainville (Turiboiru, Pamauita and Matsiogu) populations lack the light dorsal spotting and tend to have the dark pigment of the dorsum and sides concentrated through the center of the scales. This gives the appearance of dark longitudinal stripes on an only slightly lighter background.

Distribution (Fig. 2): *S. tanneri* has been collected at both the north and south ends of Bougainville (422 specimens), as well as on Shortland (1 specimen) and Choiseul (1 specimen). Altitudinally, the species is known to range from the coastal lowlands up to about 3000 feet.

Variation: The variation of several meristic characters is summarized in Table 1.

The degree of contact between the prefrontals ranges from a broad median suture to a bare "point contact" at their inner angles. In only a single specimen of the whole series, however, do the prefrontals just fail to meet at their inner angles. In the majority of specimens, the line of contact is at least one-third to one-half the length of the prefrontal.

Large, symmetrical nuchal scales are definitely lacking, although the sporadic occurrence of one or more (serial) large, transverse scales in the 4-5 scale rows posterior to the parietals (Fig. 1) suggests that perhaps the genetic basis for the formation of nuchal scales is still being variably expressed. Such a high degree of variability might well obtain in a previously well-ordered structure that was being secondarily lost.

Either the 4th or 5th supralabial may be below the center of the eye. When it is the 4th supralabial, either the 2nd or 3rd supralabials have fused to form a scale as long as the first supralabial or a small wedge-shaped scale may project between the 2nd and 3rd supralabial, thus separating them except along the edge of the lip where they remain in contact. In most individuals, however, the 5th supralabial is below the center of the eye.

The 4th supralabial occurs below the center of the eye with greater frequency in the populations from southern Bougainville (Turiboiru, Pamauita and Matsiogu = 37%) than in the populations from northern Bougainville (Kunua, Mutahi, Topanas,

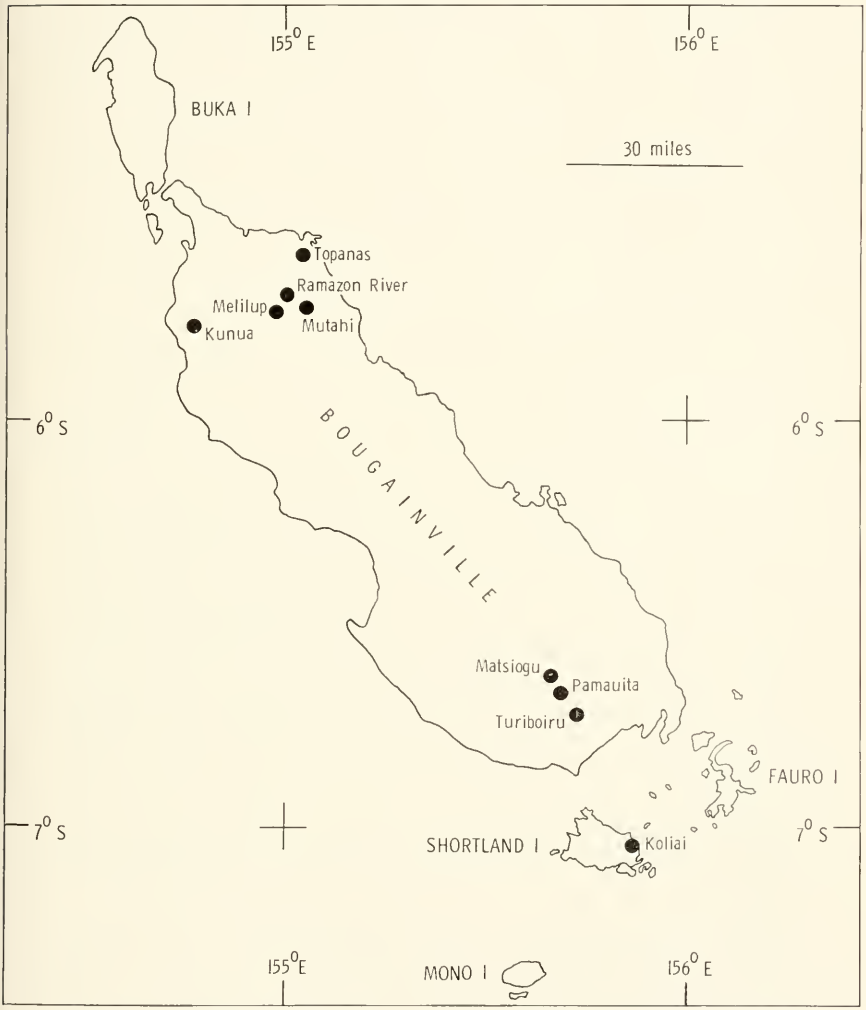

Figure 2. Bougainville and surrounding islands, showing the localities from which *Sphenomorphus tanneri* is presently known. There is also a single specimen from an unknown locality on Choiseul.

Melilup and Ramazon River = 11½%). The frequency of this trait is probably subject to clinal variation from one end of Bougainville to the other, but the rate of change per unit distance will not be known until populations from the central two-thirds of Bougainville are sampled.

This particular difference in squamation between northern and southern populations on Bougainville is made even more interesting by noting its correlation with the difference in color patterns between the two populations (see above) — the striped pattern occurring in some individuals in the south but never in the north. These differences may be taxonomically important, but their significance can not be properly evaluated until populations from intervening localities are studied.

Type specimen: The holotype has 30 scales around midbody, 16-16 lamellae beneath the 4th toe, and the 5th supralabial is below the center of the eye.

Shortland Island specimen: The single specimen from Shortland Island (Fig. 2), the only other island besides Bougainville and Choiseul from which the species is known, does not differ substantially from the Bougainville specimens. There are 30 scales around midbody and 17-17 lamellae beneath the 4th toe.

Comparisons between the Shortland population and the northern and southern populations on Bougainville would be interesting, but can hardly be carried very far at present with only one specimen available to represent the Shortland population. It is interesting to note, however, that while the Shortland specimen lacks the striped pattern characteristic of some individuals from southern Bougainville, it does have the 4th supralabial below the center of the eye on both sides of the head. This condition, as discussed above, tends to occur more frequently in lizards from southern Bougainville (37%) than those from northern Bougainville (11½%).

Choiseul Island specimen: The single specimen from an unknown locality on Choiseul (AMNH 44004) is poorly preserved but appears to differ in no significant way from Bougainville and Shortland specimens.

Habitat: On Bougainville the species is found in its greatest numbers in the swampy lowlands near the coast where small creeks spread out and intermix and where the swampy species of the *Pandanus* plant grows. The land is subject to occasional inundation during heavy rains, but there are always dry knolls onto which the reptiles and amphibians can retreat. The usual microhabitat in the swampy lowlands is under and in rotten logs and

thicker layers of decaying vegetable matter, while on higher ground and in the mountain ranges the species is usually found only living under and in rotten logs.

The Shortland Island specimen was found under a pile of decaying fronds in a coconut plantation.

Habits: S. tanneri is a burrower and shows a preference for very damp country. Other than this, little is known about the species' habits. No individual was ever seen out in the open of its own accord. It escapes by burrowing when cover is removed and it is disturbed.

Reproduction: S. tanneri is oviparous and remarkably consistent in laying only 2 eggs at a time. Of the 49 females found to be gravid with oviducal eggs, 47 had snout-vent lengths ranging from 41-50 mm (Table 1). Given the large total sample size (424 specimens) from which these females were taken, the low end of the size distribution may represent the size at which females become capable of reproducing.

Of the 49 gravid females, 47 contained 2 eggs; 46 of these held 1 egg in each oviduct and a single specimen contained 2 eggs in the right oviduct alone. Of the 2 remaining females, one contained 3 eggs, 2 in the right oviduct and 1 in the left, and a second female contained only a single well-developed egg in the right oviduct. In all cases in which there were eggs in both oviducts (47), those eggs in the right oviduct were invariably situated more anteriorly; this is apparently an accommodation for the stomach, which lies on the left side.

The 49 gravid females were collected in March (2), May (20), June (5), July (21), and December (1).

Eggs collected in the field on 17 May 1966 measured 14.8 x 8.0 (with an embryo), 13.0 x 7.5, 13.4 x 7.0 mm (unopened).

Morphological comparisons with Bougainville relatives: The only other sympatric members of *tanneri*'s species group (Table 4) on Bougainville are *Sphenomorphus solomonis* and *S. cranei*. Both species can be easily distinguished on the basis of the characters listed in Table 2.

Tanneri and *solomonis* are similar in their dorsal color patterns which consist of white flecking on a dark ground color. In *tanneri*, however, the ground color is a rich dark brown to brownish black while in *solomonis* the color of the dorsum ranges from brownish black to gray. The white spots along the dorsolateral line never coalesce to form a light line in *solomonis* as they do in *tanneri*.

The ventral color patterns of *tanneri* and *solomonis* are quite distinctive. In *tanneri* the venter of the body is immaculate while

the chin and throat are heavily pigmented. *Solomonis*, on the other hand, usually has the venter of the head and body uniformly spotted throughout, each ventral scale of the body containing a central dark spot.

The dorsal ground color in *cranei* varies from very dark dull brown to blackish brown and is patterned with thin, whitish to yellow transverse bars from the nape of the neck onto the tail.

In life the belly and underside of the tail in *tanneri* and *cranei* are often suffused with a translucent reddish color. In *solomonis* the ventral surfaces lack any reddish coloration.

Ecological comparisons with Bougainville relatives: The species most similar in ecology to *tanneri* on Bougainville is *Sphenomorphus solomonis*, one of *tanneri*'s closest relatives on the island. Both species, along with two species of *Tribolonotus* (*blanchardi* and an as yet unnamed species), are the most extreme burrowers in the Bougainville lizard fauna. *Solomonis* is much more common than *tanneri* and has a slightly greater altitudinal range — from the coast to at least 3000 feet (and perhaps up to 4000 feet) in the mountains.

Solomonis occurs in a wider variety of habitats than *tanneri*, being most commonly found in the top few inches of soil and humus and under logs in open gardens, secondary scrub, tall primary forest, dry coastal country and swampy areas. In the mountains, *solomonis* is much reduced in numbers as the altitude increases and is found mainly on the ridges and in secondary scrub. In the lowlands very large numbers of *solomonis* can be taken when logs and vegetation are being cleared off the ground for native gardens and when the topsoil is first worked.

As fewer *cranei* have been collected than *solomonis* and *tanneri*, field observations for this species are less complete than for its two closest relatives on Bougainville. *Cranei*, however, also seems to be a burrower, although much less so than *solomonis* and *tanneri*. Unlike *solomonis* and *tanneri*, *cranei* has not been collected in the lowlands, but is known from the mountains and steep-sided valleys above 500 feet where there is tall, cool primary forest. *Cranei* is much more highly dependent on water and moisture than *tanneri* and *solomonis* and is most usually found under stones, wood, or debris in small creek beds with running water or soaked beds. In this habitat it is found in company with *Tribolonotus blanchardi* and *Sphenomorphus (Parotosaurus) concinnatus*, but *cranei* is by far the least common of the three species.

Tanneri and *solomonis* are both oviparous, but the mode of reproduction in *cranei* is unknown. As noted above, *tanneri* is remarkably consistent in producing only two eggs at a time. *Solomonis*, on the other hand, produces clutches with 3-6 eggs.

Discussion: Current research (by Greer) on the delimitation and relationships of skink taxa indicates that there are several species groups now included in the genus *Sphenomorphus*. The two largest species groups of the genus are discussed below.

One of these, which may be called the *variegatus* species group (Table 3), also includes skinks of the genera *Otosaurus*, *Parotosaurus*, and *Insulasaurus* and is characterized by the following suite of external characters: well developed digits and limbs, which overlap in most species when adpressed to the body; frontal generally in contact with 3 or more of the anteriormost supraoculars; generally 5 or more supraoculars; supranasal scale (large in *Otosaurus*, small in *Parotosaurus*) or double anterior loreal present in most species, but some species with no supranasals and only a single anterior loreal[1]; nuchals lacking; high number of scales around midbody (usually 32 or more); dorsal scales subequal in size.

The other large species group within *Sphenomorphus*, the one to which *tanneri* belongs and which may be called the *fasciatus* species group (Table 4), is characterized by the following external characters: digits and limbs usually less well developed, the limbs generally not overlapping, or just slightly overlapping when adpressed to the body; frontal in contact with the anterior 2 supraoculars; 4 (much less frequently 5) supraoculars; a single anterior loreal; no supranasals; usually a series of two or more symmetrical nuchal scales; fewer scales around midbody (generally 36 or fewer); scales of the 2 vertebral rows usually broader than the other dorsal scales, i.e., they are transversely enlarged.

Whole skulls of several species of both species groups have also been examined. Both species groups display several important similarities in their skull morphology, but a discussion of these

[1] As the small supranasal of some *Parotosaurus* and the double anterior loreal of some *Sphenomorphus* may be variable in shape and form, or even present on one side of the head and absent on the other in a single individual (*Parotosaurus concinnatus*, personal observation and Burt and Burt, 1932:542), it does not seem justifiable to exclude from the *variegatus* species group those species which agree with the diagnosis except for lacking a supranasal or a double anterior loreal.

similarities is best deferred to a later date. The three important differences in skull morphology between the *variegatus* and *solomonis* groups are as follows:

variegatus group	*solomonis* group
1.) Postorbital bone lacking or very small.	1.) Postorbital bone usually long and thin.
2.) Supratemporal fenestra usually lacking or very small.	2.) Supratemporal fenestra generally well developed.
3.) No anteriorly projecting ectopterygoid process to the palatine which would exclude the palatal ramus of the pterygoid from a position on the edge of the infraorbital vacuity.	3.) Two subgroups within the *fasciatus* group: *solomonis* subgroup (Greer, 1967) with ectopterygoid process to palatine which excludes all or most of pterygoid from a position on infraorbital vacuity; *fasciatus* subgroup without anteriorly projecting ectopterygoid process to palatine.[1]

The two species groups may also be distinguished ecologically and geographically. The skinks of the *variegatus* group appear to be primarily surface dwellers, while those of the *fasciatus* group are, by and large, secretive burrowers as is *tanneri*.

Geographically, the *variegatus* group ranges from southeast Asia and the Greater Sunda Islands northeast to the Philippines and east through Celebes and the Lesser Sunda Islands to New Guinea and the Solomons. The group is not found, however, in Australia. The center of abundance for the group appears to be the western part of the Indo-Australian archipelago and, perhaps to a lesser extent, New Guinea.

The *fasciatus* group has its center of abundance on New Guinea, but extends northwest to the Philippines (*fasciatus*), west into the Lesser Sunda Islands (*emigrans* and *antoniorum*), south into northern and eastern Australia (e.g., *crassicauda, elegantulum, punctulatum* and *njöbergi*), and east into the Solomon Islands (*cranei, solomonis* and *tanneri*).

[1] *S. tanneri* lacks the ectopterygoid process to the palatine and is therefore a member of the *fasciatus* subgroup of the *fasciatus* species group of *Sphenomorphus*.

The two species groups considered here appear to be monophyletic, although convergent tendencies in both groups (e.g. the loss of nuchal scales, of transversely enlarged vertebral scales, and of the postorbital bone in the *fasciatus* group and the presence of only 4 supraoculars in the *variegatus* group) make formal taxonomic treatment difficult. For this reason the ranking and further delimitation and subdivision of the species groups will be considered at a later date.

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Mrs. Patricia H. Kerfoot made the line drawing for Figure 1 and Mr. Rick Stafford took the photograph for Figure 3.

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TABLE 1

Frequency distribution for several meristic characters in *Sphenomorphus tanneri*. N = number of specimens examined.

Midbody Scales (N = 156)

x	28	29	30	31	32
f(x)	5	5	115	11	20

Supralabial below Center of Eye (N = 415)

x	5-5	4-5	4-4
f(x)	337	43	35

Number of Lamellae beneath 4th Toe (N = 228)

x	13	14	15	16	17	18	19	20
f(x)	2	3	20	62	90	32	17	2

Snout-Vent Length of Gravid Females (N = 47)

x	41	42	43	44	45	46	47	48	49	50
f(x)	1	3	5	8	7	6	7	5	3	2

TABLE 2

Morphological differences between *S. tanneri* and its two closest relatives on Bougainville.

	tanneri	*solomonis*	*cranei*
Snout-vent length	23-52 mm	27-72 mm	29-71 mm
Scales around mid-body	28-32 (usually 30)	24-30 (usually 26-30)	32-41 (usually 34, 36)
Prefrontals meet	Yes, except in 1 of 424 specimens	No	Yes, except in 2 of 23 specimens
Supralabial below center of eye	4th (13%) or 5th (87%)	4th (< ½%) or 5th (> 99½%)	5th (11%) or 6th (89%)
Nuchal scales	Absent	Present, 2-4 pairs	Present, 3-5 pairs
Subdigital lamellae (4th toe)	13-20, usually 15-19	13-17	20-29, most usually 22-28

Figure 3. Holotype of *Sphenomorphus tanneri* (MCZ 76551), showing the light spotting on the dark brown dorsum.

TABLE 3

The *variegatus* species group of the scincid genus *Sphenomorphus* (and including the species referred to the genera *Otosaurus, Parotosaurus* and *Insulasaurus*). Species which we have examined are marked by an asterisk (*). In those instances in which no reliable data on meristic characters have been available in the literature, only data from the type description are given. The fragmented head scales of *Sphenomorphus taylori* make it meaningless to try to determine if the prefrontals meet or not.

SPECIES WITH A SUPRANASAL AND / OR DOUBLE ANTERIOR LOREAL

	Author	Range	Scales around midbody	Subdigital lamellae on 4th toe	Adpressed limbs meet	Prefrontals meet	Number of supraoculars (touching frontal)	Nuchal pairs
*taylori**	Burt, 1930	Bougainville	53-61	27-35	+	?	5-7 (3)	+ 1-2
totocarinatus	Vogt, 1932	New Guinea	50	20	+	—	6 (3)	—
*annectens**	Boulenger, 1897	New Guinea	50	21	+	—	9 (3)	—
nigrolabris	Günther, 1873	Celebes	40-50	20-27	+	+	6 (3)	—
*multisquamulatus**	Inger, 1958	Borneo	40-49	16-22	+	+	6-7 (3)	—
sarasinorum	Boulenger, 1897	Celebes	44-46	22-24	+	+	7-8 (3-4)	—

*jobiense**	Meyer, 1874	New Guinea & islands	38-46	18-29	+	+	5 (2-3)	—
*stickeli**	Loveridge, 1948	New Guinea	38-44	22-29	+	+	6-8 (3)	—
tropidonotus	Boulenger, 1897	Celebes	42-44	27	+	—	6 (3)	—
haasi	Inger & Hosmer, 1965	Sarawak	41-42	16-18	+	±	6 (3)	—
*cyanolaemus**	Inger & Hosmer, 1965	Sarawak	37-42	16-19	+	+	6 (3)	—
sabanus	Inger, 1958	Borneo	38-42	18-22	+	+	6-7 (3)	—
*wolfi**	Sternfeld, 1920	Buka	38-42	22-25	+	+	4 (2)	—
*variegatus**	Peters, 1867	Philippines	37-41	21-27	+	±	6-8 (3)	—
amblyplacodes	Vogt, 1932	New Guinea	41	27	+	+	5 (2)	+ 1
simus	Sauvage, 1879	New Guinea	40	25	+	+	6 (3)	—
mimikanus	Boulenger, 1914	New Guinea	40	15-16	+	+	7 (3)	—
*concinnatus**	Boulenger, 1887	Solomon Islands	40	22-25	+	+	4 (2)	—
anomalopus	Boulenger, 1890	Sumatra	38	16	+	+	4 (3)	—
*wrighti**	Taylor, 1925	Palawan	38	25	+	+	5 (2)	—
*granulatus**	Boulenger, 1903	New Guinea	36	20	+	+	7 (3)	—
maculicollus	Bacon, 1967	Sarawak	36	17-18	+	—	8 (4)	—

*darlingtoni**	Loveridge, 1945	New Guinea	34-36	12-15	—	+	5 (2)	—
*kinabaluensis**	Bartlett, 1945	Borneo	32-35	15-17	+	+	5-6 (2-3)	—
murudensis	Smith, 1925	Borneo	30-32	16	+	+	6 (3)	—
SPECIES WITHOUT A SUPRANASAL OR DOUBLE ANTERIOR LOREAL								
*florense**	Weber, 1890/1	Flores	44-50	27-29	+	+	6-7 (4)	—
kühuei	Roux, 1910	Kei Islands	42	34	+	+	7 (4)	—
misolense	Vogt, 1928	Misol	42	22	+	+	7 (3)	—
*arborens**	Taylor, 1917	Philippines	40-42	21	+	+	5 (3)	—
*maculatus**	Blyth, 1853	S. E. Asia	38-42	16-22	+	—	5 (2-3)	—
*striolatus**	Weber, 1890/1	Flores	40	26	+	+	7 (4)	—
*dussumieri**	Duméril & Bibron, 1839	India	40	20-25	+	+	4-5 (2-3)	—
*boulengeri**	Van Denburgh, 1912	Formosa, Hainan, S. E. China	36-40	18-20	+	±	4 (2-3)	—

*formosensis**	Van Denburgh, 1912	Formosa, S. E. China	32-38	16-20	+	±	4 (2-3)	—
lineopunctulatus	Taylor, 1962	Thailand	38	22	+	—	4 (3)	—
*indicum**	Gray, 1853	E. Asia	30-38	16-22	+	±	6 (2-3)	—
melanochlorus	Vogt, 1932	New Guinea	36	21	+	—	5 (3)	—
aignanus	Boulenger, 1898	St. Aignan	32-36	40-42	+	+	5 (3)	—
*sanctus**	Duméril & Bibron, 1839	Sumatra, Java	32-34	25-30	+	+	5 (3)	—
milnense	Boulenger, 1903	New Guinea	30-32	35-37	+	+	5 (3)	—

TABLE 4

The *fasciatus* species group of the scinid genus *Sphenomorphus*. The conventions adopted for this table are the same as for Table 3. Question marks indicate that specimens of the species were not available to us and the state of the character could not be determined from the literature.

	Author	Range	Scales around midbody	Subdigital lamellae on 4th toe	Adpressed limbs meet	Prefrontals meet	Number of supraoculars (touching frontal)	Nuchal pairs	Snout-vent length (mm)	Vertebral scales transversely enlarged
neuhaussi	Vogt, 1911	New Guinea	34-38	14	—	—	4 (1)	+ 1	89	?
*cranei**	Schmidt, 1932	Solomon Islands	32-41	22-31	+	+	4 (2)	±	71	+
*pratti**	Boulenger, 1903	New Guinea	36	13-14	—	—	4 (2)	—	87	+
*mülleri**	Schlegel, 1837	New Guinea	34	18-20	—	—	4 (2)	+ 1-2	170	+
derooyae	de Jong, 1927	New Guinea	34	24-26	?	+	4 (2)	+ 5	54	+
jeudei	Boulenger, 1914	New Guinea	34	18	—	+	4 (2)	—	61	+
wollastoni	Boulenger, 1914	New Guinea	32	17	—	—	4 (2)	+ 1	90	+
rufus	Boulenger, 1887	Aru Islands	32	20	+	+	4 (2)	—	60	+

*loriae**	Boulenger, 1897	New Guinea	30-32	16-17	—	+	4 (2)	—	66	+
*tanneri**	new species	Solomon Islands	28-32	13-20	—	+	4 (2)	—	52	—
*antoniorus**	Smith, 1927	Timor	28-32	15-19	—	±	4 (2)	± 1-2	55	—
keiensis	Kopstein, 1926	Kei Islands	31	14	—	—	4 (2)	+ 3	79	?
tornieri	Vogt, 1911	New Guinea	31	16-18	+	—	6 (2)	+ 2	71	+
nigriventre	de Rooij, 1915	New Guinea	30	16-20	—	+	4 (2)	—	90	—
*maindroni**	Sauvage, 1878	New Britain	30	28	+	+	4 (2)	+ 5	60	+
dammermani	Kopstein, 1927	Sulu Islands	30	23	+	+	5 (2)	—	61	+
unilineatus	de Rooij, 1915	New Guinea	30	15	—	—	4 (2)	+ 1-2	92	?
*fasciatus**	Gray, 1845	Philippines	28-30	22-25	—	+	4 (2)	+ 4-5	73	+
brevipes	Boettger, 1895	Halmahera, Ternate	28-30	14-16	—	—	4 (2)	+ 4-6	58	+
*nigricaudus**	Macleay, 1877	New Guinea & N. E. Queensland	26-30	16-20	—	—	4 (2)	+ 2-5	80	+
*schoedei**	Vogt, 1912	Valise	26-29	16	—	—	4 (2)	+ 1-3	60	+
nigrolineatus	Boulenger, 1897	New Guinea	28	18	+	—	4 (2)	+ 6	57	+
aruanus	Roux, 1910	Aru Islands	28	16	—	+	4 (2)	+ 4	52	+
undulatus	Peters & Doria, 1878	New Guinea & Mysore	28	20	+	+	5 (2)	+ 3-4	68	+
moszkowskii	Vogt, 1912	New Guinea	28	18	—	—	5 (?)	+ 1	31	+
longicaudatus	de Rooij, 1915	New Guinea	28	18-20	—	+	4 (2)	+ 4-5	92	+

amboinense	Kopstein, 1926	Ambon	28	18	+	+	5 (2)	+ 3-4	45	+
wirzi	Roux, 1919	New Guinea	28	18	—	—	4 (2)	+ 3	75	?
beauforti	de Jong, 1927	New Guinea	26	12	?	+	4 (2)	—	46	?
*emigrans**	Lidth de Jeude, 1894	Sumba, Samao	26	18-20	—	—	4 (2)	+ 1	58	?
*solomonis**	Boulenger, 1887	Solomon Islands	24-26	15-17	—	—	4 (2)	+ 4-6	57	+
forbesi	Boulenger, 1888	New Guinea	24-26	10	—	—	4 (?)	+ 4	59	+
oligolepis	Boulenger, 1914	New Guinea	24	12-13	—	—	4 (2)	+ 3-5	55	+
*pardalis**	Macleay, 1877	Cape York Peninsula & Islands	24	18	—	—	4 (2)	+ 3	59	+
nototaenia	Boulenger, 1914	New Guinea	24	18	+	—	4 (2)	+ 3	48	+
albodorsale	Vogt, 1932	New Guinea	24	25	+	—	?	+ 3	45	?
*schultzei**	Vogt, 1911	New Guinea	20-24	9-12	—	±	4 (2)	+ 4	30	+
*crassicaudus**	Duméril, 1851	New Guinea to N. E. Australia	22	15-18	—	—	4 (2)	+ 4	46	+
conutus	Roux, 1927	New Guinea	22	15-17	—	—	4 (2)	+ 3-4	30	+
*mjöbergi**	Lönnberg & Andersson, 1915	N. Queensland	22	12-15	—	—	4 (2)	+ 4	71	?
*pumilus**	Boulenger, 1887	Cape York	20	17-18	—	—	4 (2)	+ 4	45	+
*australis**	Gray, 1839	S. W. Australia	18-20	21	—	±	4 (2)	+ 2-3	80	—
*punctulatus**	Peters, 1871	Queensland	18-20	12-14	—	—	4 (2)	+ 1-3	55	—

BREVIORA

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THE GENERIC RELATIONSHIPS OF THE AFRICAN SCINCID GENUS *EUMECIA*

Allen E. Greer

In 1870 Bocage described a new skink (*anchietae*) from Africa that was peculiar in having an elongate body form, small appendages with a reduced number of digits (2 fingers and 3 toes), a pair of supranasals meeting behind the rostral and a spectacle in the movable lower eyelid. Bocage placed the new species in a distinct genus which he named *Eumecia,* apparently to emphasize a similarity which he believed to exist with *Eumeces.*

The three subsequent revisionary studies on scincid genera rightly recognized the closer affinity of *Eumecia* with what have come to be called the lygosomine skinks rather than with *Eumeces* or its subfamily.[1]

Boulenger (1887) placed *anchietae* in the *Riopa* section of the genus *Lygosoma,* and in 1897 described a species (*johnstoni*) from Nyasaland that was distinguishable from *anchietae* primarily on the basis of a further reduction in the number of digits (1 finger and 2 toes in *johnstoni;* 2 fingers and 3 toes in *anchietae*). Like *anchietae, johnstoni* was placed in the section *Riopa* of the genus *Lygosoma.*

Smith (1937) revived Bocage's name *Eumecia* for a subgenus of the genus *Riopa* and included in it only *anchietae* and *johnstoni.* Mittleman (1952) agreed with Smith's conception of the taxon *Eumecia* but gave it full generic rank in his classification.

Loveridge (1953 and 1957) placed both *anchietae* and *johnstoni* in the genus *Riopa* without recognizing subgenera, thus adopting

[1] The subfamily Lygosominae is characterized by a single frontal bone, and palatine bones which meet along the midline of the palate to form a secondary palate. *Eumeces* is considered to be a scincine, a subfamily characterized, in part, by a divided frontal bone, and palatines which do not meet along the ventral midline of the palate (Greer, MS).

a basically Boulengerian conception of the species' taxonomic position. The same author (1953) pointed out the very real possibility that *johnstoni* was simply a race of *anchietae* and further noted that some *anchietae* had three fingers instead of two.

That *anchietae* and *johnstoni* should be accorded separate supraspecific rank as recognized by Bocage (1870), Smith (1937), and Mittleman (1952) is suggested by the fact that they are the only African lygosomine skinks with supranasals to have fewer than 5 fingers and 5 toes. Indeed it was on this criterion that *Eumecia* has been regarded as distinct from *Riopa* and its supposed relatives.

In this paper, the two closely related species *anchietae* and *johnstoni*[1] are considered to constitute a distinct genus *Eumecia*, for reasons that will become apparent in the following discussion, and the genus is shown to be most closely related to *Mabuya* and not *Riopa*. For the purposes of this discussion *Riopa* is understood in the sense of Smith's (1937) subgenus *Riopa* and Mittleman's (1952) genera *Riopa, Squamicilia* and *Mochlus* collectively. It is not clear to me why *Eumecia* was always thought by Boulenger and later authors to be more closely related to *Riopa* and its supposed relatives than to *Mabuya*. On the basis of externals there is no one character that will serve to distinguish all *Riopa* from all *Mabuya*. There is however one external character that will distinguish some *Mabuya* from all *Riopa*, namely the relative position of the prefrontal scales, and in this regard *Eumecia* is like *Mabuya* rather than *Riopa*. The prefrontals are never in contact in *Riopa*, but they do meet medially in *Eumecia* and in about one-third of the species of *Mabuya* (surveyed from Boulenger, 1887).

Comparisons of the skulls of 30 species of *Mabuya* and 13 species of *Riopa* indicate that there are important differences in skull morphology between *Mabuya* and *Riopa*, and on the basis of skull characters *Eumecia* is clearly more closely related to *Mabuya* than to *Riopa* (Table 1).

The single greatest difference between *Mabuya* and *Riopa* is in the relationships of the bones of the palate (Fig. 1). In both

[1] I have seen neither a skull nor an alcoholic specimen of *johnstoni*, which is still known only from the type. I am assuming throughout this paper that the two species are so similar (conspecific?) that, unless stated otherwise, observations made on the two skulls and alcoholic specimens of *anchietae* are also valid for *johnstoni*, and therefore for the whole genus *Eumecia*.

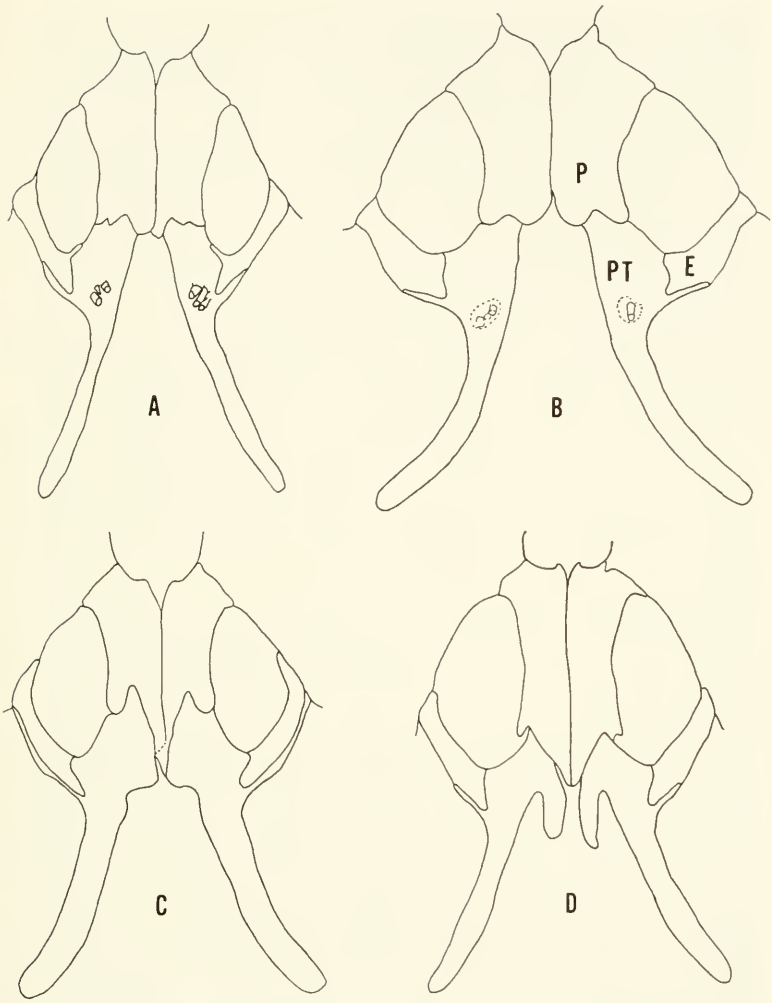

Figure 1. Ventral view of the secondary palate of: A) *Eumecia anchietae* (MCZ 41562), Kaimosi, Kakamega, Kenya; B) *Mabuya polytropis* (MCZ 8103), Krilii Cameroon; C) *Riopa punctata* (MCZ 3238), 70 miles SW of Amballa, India; D) *Leptosiaphos blochmanni* (untagged MCZ specimen), Upper Mulinga, Idjwi, Id., Congo. Abbreviations: E, ectopterygoid; P, palatine; PT, pterygoid. A and B drawn to one scale and C and D drawn to another scale.

Mabuya and *Riopa* the palatine bones meet along the ventral midline of the palate to form a secondary palate separating the air (above) and food (below) passages, a structure that is characteristic of the subfamily Lygosominae (Greer, MS). In *Riopa* the development of a secondary palate is more extensive than in *Mabuya* in that the palatal rami of the pterygoids approach but do not touch along the midline of the palate. The pterygoids are separated from each other by a pair of medial, posteriorly projecting processes from the palatines which are closely applied to the inner edges of the palatal rami and which themselves touch along the midline to close the gap between the pterygoids.

In *Mabuya,* on the other hand, and in *Eumecia,* the palatal rami of the pterygoids are widely separated and divergent, and there are no posteriorly projecting processes from the palatines (Fig. 1).

In *Eumecia* there is a broad suture between the prefrontal and nasal bones which thus separates the frontal from the maxilla. In 12 of the 23 species of *Mabuya* examined for this feature, the prefrontal articulates with the nasal, but in *Riopa* only 2 of the 12 species checked show a similar relationship of the prefrontal and nasal.

Similarly, *Eumecia* shows a short longitudinal series of pterygoid teeth, a feature shared with 17 of the 30 species of *Mabuya* examined for this character. However, *Riopa bowringi* was the only one of the 13 species of *Riopa* examined which was found to have pterygoid teeth.

Another somewhat statistical difference that aligns *Eumecia* with *Mabuya* is the number of teeth on the maxilla. The two specimens of *Eumecia anchietae* examined had 24-26 teeth on the maxilla. Only one species of *Mabuya* (*occidentalis*) of the 29 examined had fewer than 20 maxillary teeth; all others had 20 or more. Of the 13 species of *Riopa* examined for this character, however, only 4 species had 20 or more teeth on the maxilla.

The one significant similarity between *Riopa* and *Eumecia* in the gross morphology of the skull is in the common absence of the postorbital bone. *Eumecia anchietae* and the 13 species of *Riopa* examined lacked this bone while in all 29 species of *Mabuya* studied, a small, but discrete, postorbital bone was present. On the weight of the total evidence presented here, however, it would seem as if the postorbital of *Eumecia* had been lost independently of its loss in *Riopa.*

Although it seems established, on the basis of the evidence discussed above, that the relationships of *Eumecia* lie closer to *Mabuya* than to *Riopa,* it is still reasonable to ask if there might not

be a group even more closely related to *Eumecia* than is *Mabuya*.

In short, this does not seem to be the case. In Africa the only lygosomine skink which has the palatal rami of the pterygoids widely divergent and which lacks medial palatine processes projecting posteriorly as in *Mabuya* and *Eumecia* is *Ablepharus boutoni*, a relatively recent immigrant from the Australian Region. This species, however, lacks pterygoid teeth and supranasals which make it an unlikely representative of a stock ancestral to *Eumecia*.

In all African lygosomines other than *Mabuya, Eumecia* and *Ablepharus*, the palatal rami of the pterygoids are more closely apposed along the ventral midline of the palate, and medial palatine processes project posteriorly between the pterygoids. Indeed, in some African lygosomine groups with this basically *Riopa*-like palate (African *Ablepharus,* with the exception of *A. boutoni;* African *Leiolopisma; Panapsis; Leptosiaphos*), a further specialization has been the deep posterior emargination of the palatal rami of the pterygoids.

The only other groups of skinks with both supranasals and a palatal pattern generally similar to that of *Mabuya* and *Eumecia* are the genera *Emoia* and *Eugongylus*. Although these two genera are closely related[1] and are very close relatives of *Mabuya,* it seems less likely that *Eumecia* has arisen from an *Emoia–Eugongylus* stock than from a *Mabuya* ancestry.

Eumecia has pterygoid teeth and a broad surface suture between the prefrontal and nasal bones while none of the 20 species of *Emoia* or 2 species of *Eugongylus* examined had pterygoid teeth or a broad prefrontal–nasal suture. Many *Mabuya,* on the other hand, have pterygoid teeth (17 of 30 species examined) and a broad suture between the nasal and prefrontal (12 of 23 species examined).

Eumecia also has only 9 teeth on the premaxillae whereas all the *Emoia* and *Eugongylus* studied have 11 or more (12) premaxillary teeth. However, only a few *Mabuya* (6 of 30 species

[1] The species of *Eugongylus* have also been treated as relatives of *Riopa* in the three most recent classifications dealing with lygosomine skinks. Boulenger (1887) referred the species of *Eugongylus* to the section *Riopa* of the genus *Lygosoma*. Smith (1937) recognized the taxon as a subgenus of *Riopa,* and Mittleman (1952) gave the taxon full generic rank. Again, the reasons for supposing that the relationships of *Eugongylus* lay in the direction of *Riopa* are as unclear to me as those for aligning *Eumecia* with *Riopa*. On the basis of skull morphology, partly discussed here, *Eugongylus* is strikingly similar to *Emoia*. This similarity and its taxonomic significance will be discussed elsewhere.

available) have 10 or more (11-12) teeth on the premaxillae, all others have 9 (or less frequently, 8).

Furthermore, *Eumecia* is live-bearing in its mode of reproduction, as are about half the species of *Mabuya* (10 of 21 species for which information is available). In contrast, the 17 species of *Emoia* and 2 species of *Eugongylus* for which the mode of reproduction is known are all egg laying (Greer, personal observation).

Emoia and *Eugongylus* do lack the postorbital bone, as does *Eumecia,* and although *Mabuya* invariably has a small postorbital, it seems most likely, on the weight of other evidence presented above, that *Eumecia* has lost the bone independently of its loss in *Emoia* and *Eugongylus.*

The present distribution of *Mabuya* and *Eumecia* certainly supports the derivation of *Eumecia* from a *Mabuya* ancestry. *Mabuya* has obviously been in Africa a long time — long enough to have evolved numerous and diverse species. Part of this diversity is manifest in the evolution of *Eumecia* — a *"Mabuya"* with reduced appendages. In that it is the only *"Mabuya"* to have lost the postorbital bone, and to have reduced the number of fingers and toes from the primitive number of 5–5, the taxon clearly deserves generic rank.

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The following people have also contributed greatly to the present study by making available to me skulls of species not represented, or only poorly represented in the Museum of Comparative Zoology collections: Dr. Charles M. Bogert and Dr. Richard G. Zweifel, American Museum of Natural History (AMNH); Dr. Alan E. Leviton and Dr. Steve C. Anderson, California Academy of Sciences (CAS); Dr. Robert F. Inger and Mr. Hymen Marx, Field Museum of Natural History (FMNH); Dr. Charles F. Walker, University of Michigan Museum of Zoology (UMMZ).

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MATERIALS

Complete skulls of the following species have been examined.

RIOPA: afer (MCZ 41517, 41519, 71881); *bowringi* (1 from the series MCZ 26501, 26512); *fernandi* (MCZ 49696); *laeviceps* (MCZ 71889); *lineata* (AMNH 46379); *mabuiiformis* (MCZ 40267); *pembana* (MCZ 46106); *popae* (MCZ 44706); *punctata* (MCZ 3238); *sundevalli* (MCZ 41537, 41543); *tanae* (MCZ 40256); *vinciguerrae* (MCZ 17892); *albopunctata* (MCZ 8360).

EMOIA: adspersa (AMNH 29227); *atrocostata* (MCZ 15074, 15080, 26476, 26479); *boettgeri* (MCZ 22074); *callisticta* (MCZ 67203, 67308); *cyanogaster* (CAS 100684, MCZ 15121, 15135, 72278, 72287); *cyanura* (MCZ 14582, 14584, 14586, 75954, 75956); *flavigularis* (MCZ 65869); *kordoana* (MCZ 48603); *kuekenthali* (FMNH 134594); *loveridgei* (MCZ 49321); *maculata* (MCZ 49501, 49505 lot); *mivarti* (MCZ 73807, 75984); *nigra* (MCZ 15153, 15157, 67770, 72510, 72514, 72515, 72517, 72523, 75522); *pallidiceps* (MCZ 79856); *physicae* (AMNH 95772), *ruficauda* (MCZ 26482, 2 specimens, 26492); *sanfordi* (AMNH 40169); *submetallica* (AMNH 59015); *sorex* (MCZ 7705); *samoensis* (MCZ 16931).

EUGONGYLUS: albofasciolatus (MCZ 4097, 72703); *rufescens* (MCZ 49341).

EUMECIA: anchietae (MCZ 41557, 41562).

MABUYA: aurata (MCZ 56550); *bayoni* (MCZ 39731); *bensoni* (MCZ 22583); *binotata* (MCZ 22421); *blandingi* (MCZ 55171); *brachypoda* (MCZ 71410); *brevicollis* (MCZ 41306); *capensis* (MCZ 21433); *comorensis* (MCZ 24151, 2 specimens, 24155); *dorsovittata* (MCZ untagged specimen); *elegans* (MCZ 67954); *englei* (MCZ untagged specimen); *fasciata* (MCZ 37835+ 2 untagged specimens); *gravenhorsti* (MCZ 11609); *hildebrandti* (MCZ 70254, 70248); *lacertiformis* (MCZ untagged specimen); *longicaudata* (MCZ 25191); *mabuya* (CAS 71456, UMMZ 1047, MCZ 32040, 36617, 38935, 54201, 81182, 81184); *macrorhyncha* (MCZ 49551, 49552); *macularia* (MCZ 3926); *maculilabris* (MCZ 24820, 24821); *megalura* (MCZ 47611); *multifasciata* (CAS 60692 + 2 untagged specimens, UMMZ S 1830, 1831, MCZ 25198, 25199, 37843); *occidentalis* (MCZ 43180); *perroteti* (MCZ 19711); *planifrons* (MCZ 85545); *polytropis* (MCZ 8103, 54559); *quinquetaeniata* (MCZ 52424, 2 specimens, 55179, 67838, 67840); *sulcata* (MCZ 21645); *varia* (MCZ 18658, 18668, 50823, 50824, 85543).

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TABLE 1

Comparison of certain external scale (1) and skull (2-6) characters in the genera *Mabuya, Eumecia* and *Riopa* (*sensu* Smith's (1937) subgenus *Riopa* and Mittleman's (1952) genera *Riopa, Squamicilia* and *Mochlus* collectively).

	Mabuya	*Eumecia*	*Riopa*
1.	Prefrontal scales meet medially in about ⅓ of the species.	Prefrontals meet medially.	Prefrontals always separated.
2.	Palatal rami of pterygoids separated along midline of palate; no posteriorly projecting medial processes from the palatines(Fig. 1).	As in *Mabuya* (Fig. 1).	Palatal rami of pterygoids separated along midline of palate by posteriorly projecting medial processes from the palatines (Fig. 1).
3.	12 of 23 species examined with a surface suture between prefrontal and nasal bones to separate frontal and maxilla.	Surface suture between prefrontal and nasal bones to separate frontal and maxilla.	Only 2 of 13 species examined with a surface suture between prefrontal and nasal bones to separate frontal and maxilla.
4.	17 of 30 species examined have pterygoid teeth.	Pterygoid teeth present.	Only 1 (*R. bowringi*) species of 13 examined has pterygoid teeth.
5.	28 of 29 species examined have 20 or more teeth on the maxilla.	24-26 teeth on maxilla.	Only 4 of 13 species examined have 20 or more teeth on maxilla.
6.	Small to minute postorbital bone present.	Postorbital bone lacking.	Postorbital bone lacking.

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LESTIDIUM BIGELOWI, A NEW SPECIES OF PARALEPIDID FISH WITH PHOTOPHORES

Michael J. F. Graae[1]

ABSTRACT

Two specimens of a new luminous paralepidid fish were taken in the Indian Ocean during Cruise VI of the R/V *Anton Bruun*. Their main distinguishing feature is the presence of three separate and distinct, circular photophores along the ventral midline that are unlike the light organs found in other paralepidids. The two specimens are described here as a new species, and the structure of one photophore is examined in detail.

INTRODUCTION

Two evolutionary lineages, the myctophoids and the alepisauroids, are generally recognized within the pelagic members of the Myctophiformes (Iniomi). The myctophoid families Myctophidae and Neoscopelidae have discrete photophores lying in rows on each side of the ventral midline, and it has been shown recently (Haneda, 1958; Rofen, 1965) that a few members of the alepisauroid family Paralepididae have elongated luminous glands immediately on, or adjacent to, the ventral midline. One genus also has a small finger-like projection, before the eye, that may be luminous, but this organ does not appear to have the structure found in the myctophoids. This paper is concerned with a unique new species of paralepidid which, though quite similar to other paralepidids in most characters, is distinguished from them by the discrete photophores on the ventral midline.

[1] 1702 San Andres St., Santa Barbara, California.

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Lestidium bigelowi, new species

Holotype: MCZ 44881, 37.2 mm in standard length; collected during the International Indian Ocean Expedition, R/V *Anton Bruun*, Cruise VI, trawl 339A; APB label 7227; hydrographic station 339; collected in 10′ Isaacs-Kidd Midwater Trawl, depth 0-615m; 30-V-64, 0140-0645 hrs; 4°01′-4°14′S, 65°00′-65°02′E.

Paratype: MCZ 44880, 28.4mm in standard length; R/V *Anton Bruun*, Cruise VI; trawl 340B; APB label 7241; hydrographic station 340; 10′ IKMT, 0-746m; 31-V-64, 1945-0155 hrs; 5°55′-6°08′S, 64°48′-64°58′E.

Diagnosis: This species is the only paralepidid known to have light organs that are small and discrete, as opposed to long and tubular. There are three of these; all are directed ventrally. One is at the isthmus, one is between the bases of the pectoral fins, and one is just posterior to the bases of the ventral fins. In most characters, *Lestidium bigelowi* is almost intermediate between the genera *Lestidium* and *Lestidiops* (see Table 1).

Description: The following description is based on both types. Body long and slender, very compressed. Keel present for short distance ventrally between anus and anal fin. Anus between tips of appressed ventral fins. Skin smooth; scales absent, with lateral line ossicles insufficiently ossified to be observed. Lateral line extending along side of body from edge of operculum to a vertical with first of procurrent caudal rays, and slightly above middle of body.

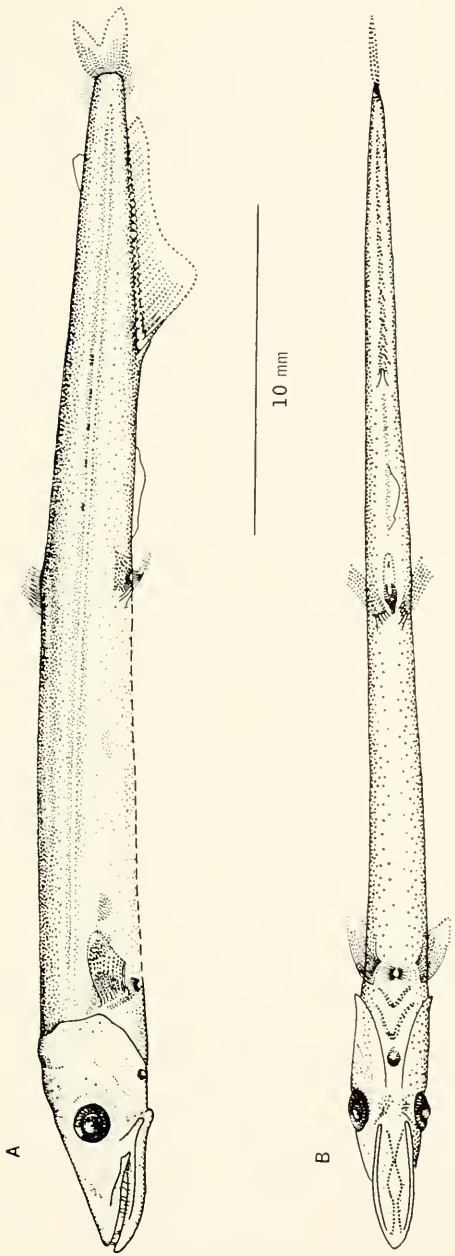

Figure 1. Side and ventral views of *Lestidium bigelowi*, new species, drawn from the holotype — 37.2 mm in standard length (MCZ 44881).

Three luminous organs on the midventral line — one at isthmus, another between bases of the pectoral fins, and the third between bases of ventral fins and anus. Isthmal and pectoral organs imbedded in flesh; anal organ close to skin, possibly open to surface or connected to rectum. In alcohol, these organs are black with a translucent, white layer at center (see discussion of luminous organs, below).

Head pointed and moderately long, widest just posterior to eyes. Snout length slightly more than two in head, about three-quarters as wide as head. Eye and pupil large, about five in head length; eye and pupil round; adipose eyelid present. Interorbital slightly concave, with two lateral, compressed, longitudinal ridges on each side. Occiput rounded, convex. Nasal apertures approximately halfway between tip of snout and eye. Opercle with posterior edge moderately pointed and notched about pectoral fin base. Mouth large, lower jaw with a slight non-ossified projection. Premaxillary extending to a point beneath anterior edge of orbit. Premaxillary with two or three depressible canines, posteriorly followed by fixed teeth. Palatine with a few depressible teeth. Gill rakers present but poorly developed on first two arches.

Dorsal fin origin slightly anterior to origins of ventral fins, a little more than halfway back on body. Posterior edge of adipose fin anterior to caudal peduncle, slightly before last anal fin ray. Inner rays of ventral fins distinctly longer than the outer. Ossification is too incomplete to permit radiographic study of vertebral column or study of lateral line ossicles through staining.

In ethyl alcohol the body is largely colorless. Melanophores, most of them stellate, cover many parts of the fish: the occiput, the edges, ridges and sutures of the jaws, the angular bone, the dorsum, the posterior part of the caudal peduncle, the ventral midline between the anus and the anal fin, the first pectoral and anal fin rays, and the anal and caudal fin ray bases. The angular bone is also covered by heavy black pigment, and the dorsum is covered by light brown pigment in a band becoming denser and darker posteriorly. Three anterior and one posterior peritoneal sections are relatively clearly outlined; the others are indistinct.

All measurements and counts are given in Table 1, and reconstructed lateral and ventral views of the holotype are shown in Figure 1.

This new species is named in honor of Dr. Henry Bryant Bigelow, to whom I wish to express my sincere thanks for his kindness and generosity.

Distribution: Taken only in the Indian Ocean, approximately 650 miles northeast of Madagascar at a depth above 750m.

TABLE 1

Proportional Measurements in Percent of Standard Length

	Lestidium bigelowi	*Lestidium atlanticum*	*Lestidiops jayakari*	*Lestidiops indopacificum*
Head length	20.8-21.8	22.4-22.9	18.5-22.0	20.3
Snout length	8.9-9.2	10.1-12.4	7.6-10.2	7.1
Snout to anus	59.9-60.0	59.8-64.1	55.7-64.6	58.4
Snout to dorsal fin	54.3-54.9	56.3-60.0	56.5-61.0	53.9
Snout to anal fin	75.0-77.4	75.4-79.2	76.7-79.4	76.8
Snout to ventral fin	56.0-56.2	56.8-59.6	48.4-58.0	54.8
Dorsal fin to ventral fin	1.4-1.6	0.0-0.5	2.3-6.5	0.9*-1.2*
Dorsal fin to anal fin	15.5-18.8	19.8-20.0	19.6-22.1	22.0*-22.9*
Dorsal fin rays	9-10	9-10	10	10
Anal fin rays	28-29	29-30	28-30	29-32
Body depth	8.5-8.9	8.0	6.7-9.1	10.0
Caudal peduncle depth	3.2-3.5	2.4-2.7	2.3-3.2	—
Eye diameter	4.0-4.6	3.9-4.4	3.4-4.9	4.5
Upper jaw length	9.7-10.9	10.3-10.5	8.2-10.0	—
Premaxillary to eyes	0.7-0.8	1.4-2.2	0.5-1.4	—
Dorsal fin to caudal fin	41.7-45.1	35.9-36.7	35.2-40.0	41.9[x]
Anal fin to caudal fin	5.9-6.0	5.2-5.9	5.3-6.5	1.9
Adipose fin to caudal fin	6.3-8.3	5.5-5.8	5.1-7.0	2.6
Dorsal fin base length	4.8-5.3	3.6-4.4	3.6-5.0	4.2
Anal fin base length	18.8-19.4	15.2-17.5	15.7-18.5	19.0

* Taken from Ege's illustration.

[x] Computed from: total length — (predorsal + dorsal base length).

Relationships: In relative proportions and numbers of fin rays, *Lestidium bigelowi* closely resembles *Lestidium atlanticum* Borodin, *Lestidiops jayakari* (Boulenger), and *Lestidiops indopacificum* (Ege). The ranges of meristic characters shown by the species in these two genera provide no grounds for separation. Analysis is further impaired by discrepancies evident in the monograph recently published by Rofen (1965), for the proportionality data provided in certain of his tables (e.g., table XXIV, pp. 302-303) are at variance with those reported in his description (e.g. that of *Lestidium atlanticum* on pp. 308-309). The single valid and conservative character which does separate *Lestidium* from *Lestidiops* is the presence or absence of an internal light organ; hence the species described here is relegated to *Lestidium.* The meristic data taken from this species are compared in Table 1 with those for *Lestidium atlanticum* and *Lestidiops jayakari* taken from Rofen's description (1965: 308, 348), and for *Lestidiops indopacificum* taken from Ege (1953).

Anatomy of the luminous organs: The three organs differ somewhat from one another in gross morphology. The anterior one (the isthmal) is buried in the muscle of the isthmus (Fig. 1A, B). It has a black cup-shaped structure with the opening directed

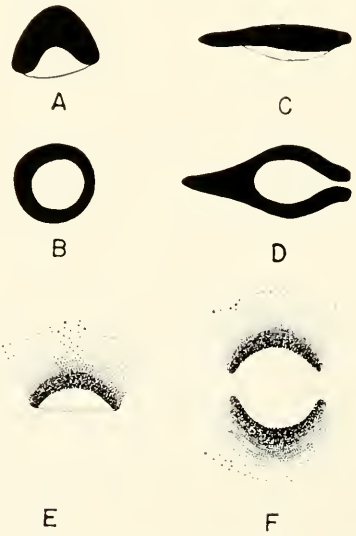

Figure 2. Photophores of holotype: A and B, lateral and ventral views of isthmal photophore; C and D, lateral and ventral views of anal photophore; E and F, lateral and ventral views of pectoral photophore.

posteroventrally and is covered by a mass of translucent tissue (Fig. 2A, B). The middle one (the pectoral) is nearer the surface than the isthmal (Fig. 1A). It too has a black, ventrally directed cup, covered with a translucent cap; its black pigment seems to be associated with the peritoneal lining (Figs. 1A, B; 2E, F). The posterior one (the anal) is close to, or partially embedded in, the skin (Fig. 1A, B). As seen from the ventral side, it has an arrowhead-shaped mass of black tissue surrounding a central translucent cap (Figs. 1B; 2C, D). There may be an opening directed posteriorly toward the anus or the surface from the central part of this photophore (Fig. 2D).

The isthmal photophore of the paratype was removed, and sectioned by William O'Day, using the following procedure: the fish was fixed whole in formalin aboard ship, and then transferred to 72% ethanol for preservation. The photophore was excised and dehydrated for twenty-four hour periods in 100% ethanol, 100% n-propanol, and 100% n-butanol. It was then infiltrated in one cc of pure glycol methacrylate with a polymerization catalyst, and transferred to fresh monomer and polymerized in a gelatin capsule at 60°C. After polymerization, the sections were cut vertically through the photophore at one micron thickness by a Porter-Blum microtome. The sections were stained first with 4% acid fuchsin in water for four minutes, and then with a concentrated solution of toluidine blue in water for five minutes. The sections were mounted on a slide and covered with a Permount cover slip (see Ashley and Feder, 1966).

The isthmal light organ (Fig. 3) is a classical example of a photophore (e.g. see Brauer, 1908, fig. XXX). It consists of a cup of heavy black pigment surrounding an internal body of granular tissue. On examination under high magnification the latter material does not seem to be associated with bacteria, implying that the luminescence of at least this organ is glandular in nature. The cup is closed ventrally by a lens-like layer of cells which separates the luminous tissue from a gelatinous cap. This cap completely covers the ventral aspect of the photophore and may serve to filter, focus, or disperse the light emitted.

The structures of the light organ resemble those found in other fishes, especially the myctophoid inioms. They do not appear to be similar to those described by Haneda (1958) for *Lestidium prolixum* Harry or *Lestrolepis japonicum* (Tanaka). They do, however, look like those found in the family Myctophidae except for the presence of an internal lens. However, since the Paralepididae are so dissimilar to the Myctophidae in other respects, the similarity of the photophore of *L. bigelowi* to those of

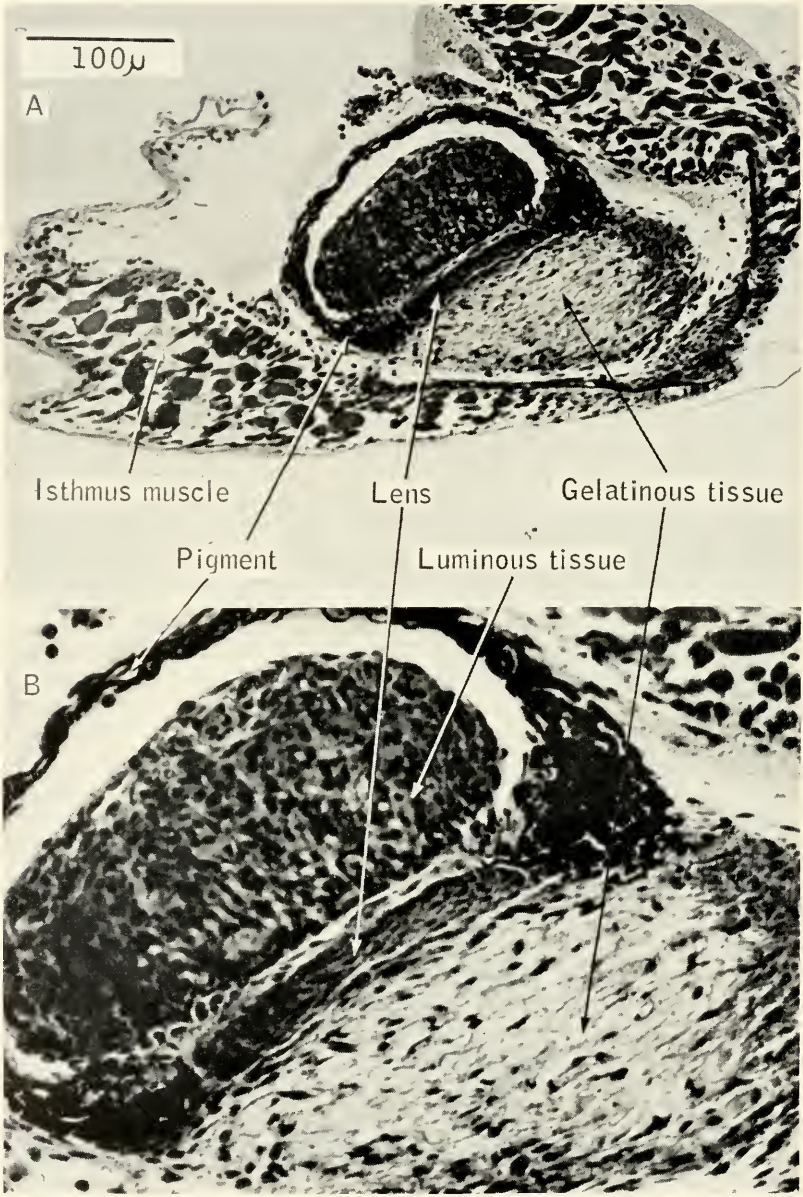

Figure 3. A, a vertical section through isthmal photophore. B, the photophore above, enlarged.

the myctophids is assumed to be due to convergence rather than to close relationship.

The anal photophore of *Lestidium bigelowi* is similar in shape to that discussed by Bertelsen, Theisen, and Munk (1965) for the argentinoid fish, *Rhynchohyalus natalensis* (Gilchrist and von Bonde). Like that of *R. natalensis,* the anal photophore of *L. bigelowi* may be connected to the anus (though posteriorly instead of anteriorly), and its luminescence may thereby also be bacterial in nature. As the anal photophore on the holotype was the only one found, the paratype being mutilated in that region, no sections were made of it; thus the question of whether this luminescence is bacterial or glandular can not now be answered.

SUMMARY

A new species of *Lestidium* was collected in the Indian Ocean in 1964. It most nearly resembles *Lestidium atlanticum* Borodin in proportions and counts, and in some other respects is similar to *Lestidiops jayakari* (Boulenger) and *L. indopacificum* (Ege). It differs from all other paralepidids in possessing discrete photophores. These photophores have a darkly pigmented cap, with opening directed ventrally, and are covered by a gelatinous, translucent mass of tissue. Photomicrographs of the isthmal photophore of the paratype show that it is very similar to those of the Myctophidae, differing significantly only in the possession of an internal lens. This similarity is attributed to convergence rather than to close relationship.

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BREVIORA

Museum of Comparative Zoology

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NOTES ON THE EMBERIZINE SPARROW *RHYNCHOSPIZA STOLZMANNI*

Raymond A. Paynter, Jr.

Rhynchospiza stolzmanni Taczanowski has one of the most restricted ranges of any of the continental Emberizinae. It occurs on the arid western slopes of the Andes in Loja, southwestern Ecuador, and from Tumbes to Cajamarca, northern Peru, or from approximately Lat. 3° 30′S to Lat. 7° 15′S. Its altitudinal range is roughly from 100 to 1,100 meters. Judging from the comparatively few specimens in collections, the species appears to be uncommon, but this may be a deceptive indicator. It seems more probable that it has a restricted habitat and is secretive, two characteristics which would make it difficult to collect.

FIELD NOTES

In mid-October 1965 I saw the species briefly at Yamana (alt. *ca.* 1,100 m), near the head of the arid Casanga Valley in southwestern Loja, Ecuador. Although these observations are only an introduction to the species, they supplement the short notes made by Jelski and Stolzmann (Taczanowski, 1886) nearly a century ago, which are the only published field observations of this interesting bird.

On several days while walking along a path on a steep hillside, my attention was occasionally attracted by the short loud calls of two or three birds concealed in sparsely distributed patches of thick brush on the lower side of the hill. A few times I was able to glimpse a dark, heavy-set bunting on the ground or in the lowest branches of the shrubs. The birds were extremely shy and silently moved downhill almost as soon as I sighted them. Late one morning a flock of about six birds was seen at a distance on the path and adjacent to a fence made of piled thorny brush. The flock quickly darted into the fence in the manner of *Zonotrichia capensis*,

which is surprisingly wary in rural areas, unlike its tame and trusting behavior in Andean cities and towns. *Z. capensis* had been collected in the fence previously and, believing this to be another flock of that species, a bird was shot as it emerged from the top of the brush pile. On recovering the specimen it was found to be *Rhynchospiza stolzmanni*, the elusive bird I had glimpsed on earlier occasions. The presence of both *Z. capensis* and *R. stolzmanni* in the same habitat is contrary to the observations of Jelski and Stolzmann (Taczanowski, 1886), who stressed the exclusion of one species in the presence of the other.

That afternoon the flock was in the same area but was even more elusive than in the morning. On the following day a loose flock of about a dozen *R. stolzmanni* was discovered a short distance away in a weedy area interspersed with leafless, lightly branched shrubs about 10 feet tall. Some of the shrubs bore pea-sized dark purple fruit. The birds were feeding on the fruit high above the ground and were completely exposed, in striking contrast to their earlier behavior. They were watched for about an hour and could be approached to within 20 or 30 feet before they were disturbed; then they merely moved a short distance and resumed feeding. Several specimens were collected here, and later a single bird was taken from a small, fully leafed tree standing alone in an area of dense underbrush. These observations are again at variance with those of Jelski and Stolzmann (Taczanowski, 1886) who saw the species only on the ground or in the lowest branches of bushes; doubtless the presence of fruiting shrubs altered the usual retiring behavior of the bird.

The birds were moderately vocal. The calls were a single loud, metallic *cheep* and, less frequently, a series of three or four *cheeps* given in rapid succession and descending tone.

Six specimens were collected at Yamana. All were in very fresh plumage and their gonads were small. Five of the series had consumed the purple fruit which stained their intestines nearly black; the sixth bird was collected a day earlier and its stomach contained only a few small seeds.

TAXONOMIC NOTES

When describing *stolzmanni*, Taczanowski (1877) placed the species in the genus *Haemophila* (= *Aimophila*) but without giving his reasons for doing so. Presumably he thought its relationship too obvious to require amplification. However, in 1898.

Ridgway created the monotypic genus *Rhynchospiza* for *stolzmanni*, noting that while the species resembles the shorter tailed, stouter billed species of *Aimophila* in several respects, it differs from them in having a tail which is much shorter than the wing, in having a "nearly even" tail, and in having very small, circular nares nearly concealed by feathers.

The generic allocation of the species has been generally accepted. Chapman (1926) apparently had unexpressed doubts about the validity of the genus when he remarked on the close resemblance between *stolzmanni* and *Aimophila sumichrasti* of Mexico, and suggested that *stolzmanni* may have had a Middle American origin. Hellmayr (1938) also mentioned the similarity between these two species but felt the short, nearly square, tail and (adding two new characters) "broader and less rounded" rectrices were "good taxonomic characters" for maintaining *Rhynchospiza* apart from *Aimophila*. In his survey of *Aimophila*, Storer (1955) briefly noted Chapman's suggested origin of *stolzmanni* but did not further consider *Rhynchospiza*.

The supposed generic characters of *Rhynchospiza* seem to me to be either inconsistent or of dubious value. The nares of *Rhynchospiza* are small, rounded, and rather concealed, but similar nostrils are found in several of the *Aimophila*, such as *strigiceps* and *rufescens*. I fail to appreciate why Ridgway and Hellmayr believed *Rhynchospiza* has a squarer tail than that of *Aimophila*. While it is true that most species of *Aimophila* have a comparatively rounded tail, the outer rectrices are long in *A. sumichrasti* and *A. ruficeps* and their tails are as square as that of *R. stolzmanni*. Hellmayr's belief that *Rhynchospiza* could be distinguished from *Aimophila* by its broad, blunt rectrices seems to have resulted from an observational error. Several species of *Aimophila* have rectrices which are rather narrow and pointed, in contrast to the condition in most emberizines, but other members of the genus have "normal" rectrices. Among the species whose tail feathers are broad and blunt, like those of *R. stolzmanni*, are *A. mystacalis, quinquestriata, sumichrasti, ruficeps*, and *rufescens*.

The only character clearly differentiating *R. stolzmanni* from all species of *Aimophila* is the tail, which averages about 12 mm shorter than the wing, while in the aimophilas the tail is at least equal to the wing, and usually considerably longer. While a short tail may be biologically advantageous, or at least not deleterious, to *R. stolzmanni*, it does not seem that a single character of this nature is of value in delimiting genera. If one were to accept a short tail

as a generic character it would follow that the notably long-tailed *A. strigiceps,* isolated in Argentina, would have to be set apart in a genus of its own, a suggestion no one has yet made. I propose, therefore, that *stolzmanni* be returned to the genus *Aimophila.*

AFFINITIES OF *AIMOPHILA STOLZMANNI*

Storer (1955) groups the species of *Aimophila* into three assemblages. First, that of *mystacalis, humeralis, ruficauda, sumichrasti,* and *strigiceps,* all large forms inhabiting arid tropical scrub, which have dark transocular stripes, rufous shoulder patches, breast bands (either pronounced or muted), and inconspicuously colored feathers on the underside of the bend of the wing. Second, a group consisting of *aestivalis, botterii, petenica* (which I consider conspecific with *botterii*), and *cassinii.* These are all smaller birds, morphologically fairly similar, which inhabit temperate grasslands and which have no dark eye stripe, no breast bands, and no pronounced shoulder patches, but do have bright yellow feathers at the wrist joint. The third division consists of the dissimilar species *quinquestriata, carpalis, ruficeps, notosticta,* and *rufescens,* a group of uncertain affinities, which lack eye stripes, shoulder patches, and conspicuously colored wrist feathers.

A. stolzmanni fits well with the first group, except for distinctive yellow feathering at the angle of the wing. It is doubtful, however, if the presence or absence of such markings may be used to assess phylogenetic relationships. Conspicuously colored (or patterned) underwing patches, which apparently function as signals in threat display, and perhaps in courtship display, are found in many families. They occur rather frequently in the Emberizinae and often are the only bright feathers on an otherwise sombre-colored bird. A cursory survey of the emberizines seems to indicate that this character is most pronounced in secretive species which inhabit grasslands, dense undergrowth, or dark habitats — areas where an inconspicuous species might effectively use a bright patch of color as a signal. If this is the case, such markings probably evolve rather readily in certain habitats and are useless to the taxonomist searching for evolutionarily conservative characters which may be clues to phylogenetic relationships. For this reason, the possession of yellow feathering at the bend of the wing is no deterrent for considering *A. stolzmanni* a member of the group containing *mystacalis, humeralis, ruficauda, sumichrasti,* and *strigiceps.*

Although *stolzmanni* bears a close resemblance to *sumichrasti,* and occupies a similar habitat, the former may not necessarily have

arisen from the latter. *A. strigiceps,* the only other South American *Aimophila,* also bears a strong resemblance to *sumichrasti.* Thus we find three species (*sumichrasti, stolzmanni,* and *strigiceps*), all with restricted ranges, which are markedly similar to one another. The restricted ranges and morphological resemblances suggest that these are relict forms; they may be older than the three boldly marked species with which they seem allied, viz. *mystacalis, humeralis,* and *ruficauda.* Their origin may be postulated as follows: In pre-Pleistocene times a simply patterned ancestor, with an incipient breast band and rufous wing patches, may have ranged from Mexico south to southern South America. During a Pleistocene interglacial period the Central American population became isolated, owing to the formation of water gaps, and differentiated into *ruficauda.* In South America the population retreated to arid refugia in Argentina and in southern Ecuador and northern Peru, forming *strigiceps* and *stolzmanni,* while the Mexican population (*sumichrasti*) was isolated to the north of the Isthmus of Tehuantepec. During a glacial period, when the sea receded, *ruficauda* spread northward into Mexico, occupying the range of *sumichrasti* and beyond, becoming isolated during later interglacials and further differentiating into the even more boldly patterned species *mystacalis* and *humeralis* on the Mexican Plateau. Movement of *ruficauda* to the south beyond northern Costa Rica was prevented because of the absence of dry scrub, thus leaving *stolzmanni* and *strigiceps* isolated in South America.

ACKNOWLEDGMENTS

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A SECOND SKINK WITH FRAGMENTED HEAD SCALES FROM BOUGAINVILLE, SOLOMON ISLANDS

Allen E. Greer and Fred Parker [1]

One of the most unusual skinks to come out of the Solomon Islands is *Sphenomorphus taylori* from the island of Bougainville. At the time of its description (Burt, 1930; based on 2 individuals from "Bougainville") the species was unique among skinks in having many of the normally large and symmetrical head scales broken up into a less ordered array of smaller scales (Fig. 3; fig. 21 in Burt and Burt, 1932). Eight more specimens of this species recently collected by Parker on Bougainville confirm that the fragmentation of the head scales is the normal condition for the species.

During the same collecting efforts that yielded *S. taylori,* seven individuals of an as yet undescribed species of skink were taken by Parker on Bougainville. Among the distinctive features of this new species is the rather symmetrical fragmentation of the head scales on the dorsal and lateral surfaces of the snout.

Although the presence of a supranasal scale would place the new species in either the genus *Otosaurus* or *Parotosaurus* in any of the most recent classifications of lygosomine skinks (Boulenger, 1887; M. A. Smith, 1937; Mittleman, 1952), recent work (by Greer; see Greer and Parker, 1967) on skink systematics indicates that these genera (along with the monotypic *Insulasaurus*) are not readily separable from a large group of *Sphenomorphus* (also see Burt and Burt, 1932: 542). Until the systematics of this group is better understood, we choose to reject the names *Otosaurus, Parotosaurus* and *Insulasaurus* in favor of *Sphenomorphus.*

[1] Department of District Administration, Kundiawa, Territory of New Guinea.

The new species may therefore be known as:

SPHENOMORPHUS FRAGOSUS new species[1]

Holotype (Fig. 1): Museum of Comparative Zoology 92265, collected by Fred Parker on 31 March 1966 at Lake Loloru (elev. 4300 feet), Bougainville, Solomon Islands.

Paratypes: Mutahi area (4000 feet), Bougainville: MCZ 92268, coll. 13 May 1966. Lake Loloru: MCZ 92262-92264, 92266-92267, same data as holotype.

Diagnosis: S. fragosus is a member of the *variegatus* species group (Greer and Parker, 1967), which is characterized by the presence of a large or small supranasal, and/or a double anterior loreal (although some species lack supranasals and have only a single anterior loreal); usually 5 or more supraoculars of which usually 3 or more are in contact with the frontal; digits and limbs well developed and generally overlapping broadly when adpressed to the body; and the absence of transversely enlarged vertebral scales, i.e., the middorsal scales are subequal in size.

The *variegatus* species group includes all the species previously referred to the genera *Otosaurus, Parotosaurus* and *Insulasaurus* as well as part of the genus *Sphenomorphus*. Those species of the *variegatus* species group with a supranasal and/or double anterior loreal are as follows: *amblyplacodes, annectens, anomalopus, celebense, concinnatus, cumingi, curtirostris, cyanolaemus, darlingtoni, granulatus, haasi, jobiense, kinabaluensis, maculicollus, mimikanus, multisquamulatus, murudensis, nigrolabris, sabanus, sarasinorous, simus, stickeli, taylori, totocarinatus, tropidonotus, variegatus, wrighti.* Those members of the *variegatus* species group lacking both a supranasal and double anterior loreal are: *aignanus, arborens, boulengeri, dussumieri, florense, formosensis, indicus, kühnei, lineopunctulatus, maculatus, melanochlorus, milnense, misolense, sanctus, striolatus.*[2]

S. fragosus can be easily distinguished from other species of its species group by means of the small symmetrical scales on the

[1] The species name calls attention to the rather symmetrical fragmentation of the head scales on the dorsal and lateral regions of the snout.

[2] The *variegatus* species group is distributed from southeast Asia and the Greater Sunda Islands northeast to the Philippines and east through Celebes and the Lesser Sunda Islands to New Guinea and the Solomon Islands. The group is not found in Australia, however. The center of abundance for the group appears to be the western part of the Indo-Australian archipelago and, perhaps to a lesser extent, New Guinea.

dorsal and lateral surfaces of the snout (Fig. 1). In this more or less symmetrical fragmentation of the scales of the snout, *S. fragosus* is unique among lygosomine skinks with the exception of the much larger *S. taylori,* also from Bougainville (for other differences between the two species, see Table 1).

Description: Body brownish above and in form tending toward stockiness; snout obtusely rounded and deep; limbs pentadactyl, well developed and overlapping when adpressed to the body (tip of 4th toe to forearm); snout-vent length of seven known specimens from 31-73 mm.

Rostral as deep as wide, projecting only slightly onto dorsal surface of snout; nostril in a single nasal; nasal bordered ventrally by the first supralabial, anteriorly by the rostral, dorsally by a thin supranasal, which touches the rostral, and posteriorly by 2 superposed anterior loreals, the upper of which contacts the supranasal; a small frontonasal is bordered anteriorly by the rostral and laterally by the supranasals; posteriorly the frontonasal is followed by a pair of small scales, and either a single small median scale and another pair of small scales, or simply by a single median scale; these small scales on the dorsal area of the snout separate the prefrontals (Fig. 1).

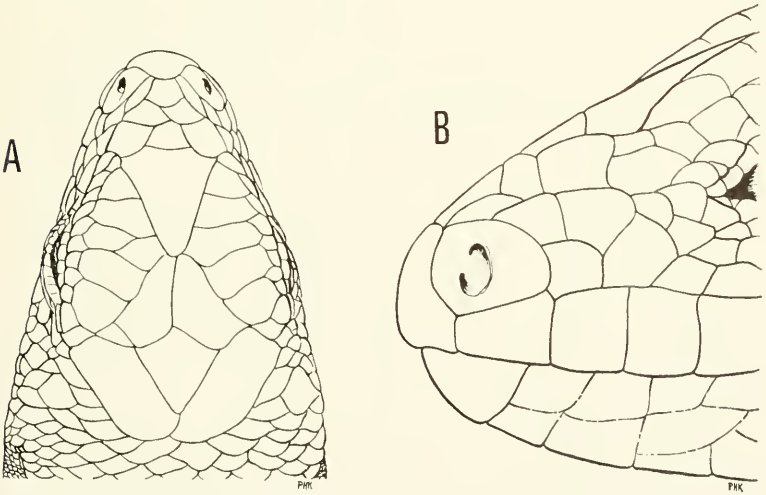

Figure 1. Holotype (Museum of Comparative Zoology 92265) of *Sphenomorphus fragosus.* A) Dorsal view of head. B) Lateral view of the left side of the snout anterior to the eye.

Frontal scale contacts the last small scale or pair of scales of the snout; the 2 superposed anterior loreals are followed by a superposed pair of posterior loreals which are directly below the prefrontal; 5 supraoculars, the 3 anteriormost supraoculars in contact with the frontal; frontoparietals and interparietal distinct; parietals meet behind interparietal; no nuchals; lower eyelid scaly, separated from supralabials by a complete row of subocular scales; 5th and 6th supralabials, or, less frequently, just 6th supralabial below eye; ear opening vertically elliptic, without lobules, and approximately equal in size to eye opening.

Scales in 42-46 longitudinal rows at midbody; dorsal body scales subequal, i.e., vertebral scales not transversely enlarged; a pair of enlarged preanal scales; 3 median series of subcaudal scales subequal in size; 4th (longest) toe with 18-21 laterally keeled subdigital lamellae; upper surface of 4th toe covered by 1 or 2 scale rows distally, 3 scale rows along the mid-section and 4-5 scale rows basally (most similar to Group V of Brongersma, 1942).

Color: In preserved specimens the upper surface of the head and body is brown with a series of more or less transversely confluent dark brown to black spots on the body which may be confined to the midline or, less frequently, extend the width of the brown dorsal area. The brown dorsum is bordered laterally by a black dorsolateral band, which is distinct but not sharply demarcated, and extends from the posterior corner of the eye to the base of the tail. The upper part of this black dorsolateral band is bordered by thin longitudinal streaks of white which tend to be more confluent and well defined in the area just above and posterior to the shoulder.

Below the black dorsolateral band the sides of the neck and body are grayish brown and, in some specimens, sporadically spotted with whitish flecks. The gray-brown of the sides fades to gray-white on the venter. The venter from the chin onto the tail is grayish white (yellow in life) and may be spotted with black.

The upper surfaces of the limbs are brown but heavily spotted with black, and the lower surfaces are white and lightly spotted with black.

The color pattern of the tail vaguely reflects the body pattern, i.e., brown middorsally with a series of dark brown to black spots dorsolaterally below which a gray ground color gives way to a gray-white venter. The regenerated tail is light reddish brown and generally unpatterned.

In juveniles the dorsum is a lighter golden brown which accentuates the dark dorsal spots and the dark sides.

Distribution (Fig. 2): The seven known specimens of *S. fragosus* are from between 4000-4300 feet, in the central highlands of Bougainville. Six specimens were taken in southcentral Bougainville (Lake Loloru, 4300 feet) and the seventh was collected in northeastern Bougainville (near Mutahi, 4000 feet). The 2 localities are approximately 70 miles apart.

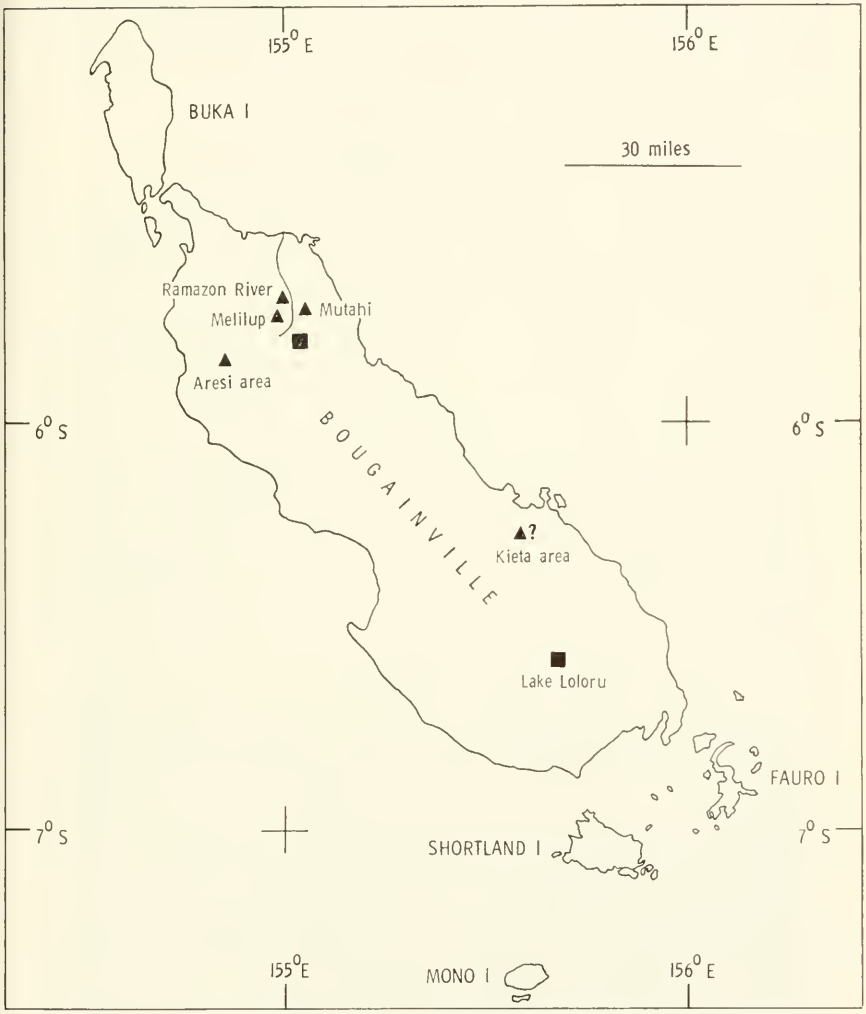

Figure 2. Map of Bougainville, Solomon Islands, showing the known collecting localities for *Sphenomorphus fragosus* (squares) and *S. taylori* (triangles).

Variation: The six specimens from southcentral Bougainville have 42(3), 43(1), 44(1), or 46(1) longitudinal scale rows around midbody. The single specimen from northeast Bougainville has 46 scales around midbody.

The color pattern of the individual from northeast Bougainville differs from the patterns of the specimens from the southcentral part of the island in that the black dorsolateral band becomes less distinct on the posterior half of the body and the light throat and chest are reticulated with black. In addition there is a dark midventral line.

MORPHOLOGICAL COMPARISONS WITH RELATIVES ON BOUGAINVILLE

The only species of *S. fragosus*' species group (see Diagnosis) on Bougainville, or in the Solomon Islands, for that matter, are *S. concinnatus* and *S. taylori*. The three species are readily distinguished by the characters given in Table 1.

S. concinnatus is widely distributed throughout the Solomon Islands from Buka Island in the northwest to Guadalcanal in the southeast. Specimens from Bougainville and neighboring islands (e.g., Buka and some of the islands in Bougainville Straits) show a good deal of inter- and intra-population variation in squamation and color pattern, indicating that the systematics of the species in the Solomons is probably not as straightforward as the simple binomial would indicate. A discussion of the variation of the species on Bougainville and in other parts of the Solomons will be the object of a separate study. The data given in Table 1 for *S. concinnatus* were obtained from 60 specimens collected at Mutahi (2200-3200 feet elev.), Bougainville.

To date, *S. taylori* (Fig. 3) has been known in the literature from only the two type specimens discussed in the original description (Burt, 1930). Parker, however, has recently obtained 8 more specimens of this species from the following localities on Bougainville (Fig. 2): Aresi area (1 specimen, 2500 feet); Kieta area (1 specimen, no exact locality data); Melilup (2 specimens, 3000 feet); Mutahi (3 specimens, 2200-3200 feet); Ramazon River (1 specimen, 1600-2400 feet). Data from these specimens are combined in Table 1 with the data from the original description of the species.

The color patterns of the three species are distinctive and immediately diagnostic. *S. concinnatus* shows some geographic and altitudinal variation in pigmentation and color pattern with specimens from the highlands of Bougainville most closely resembling

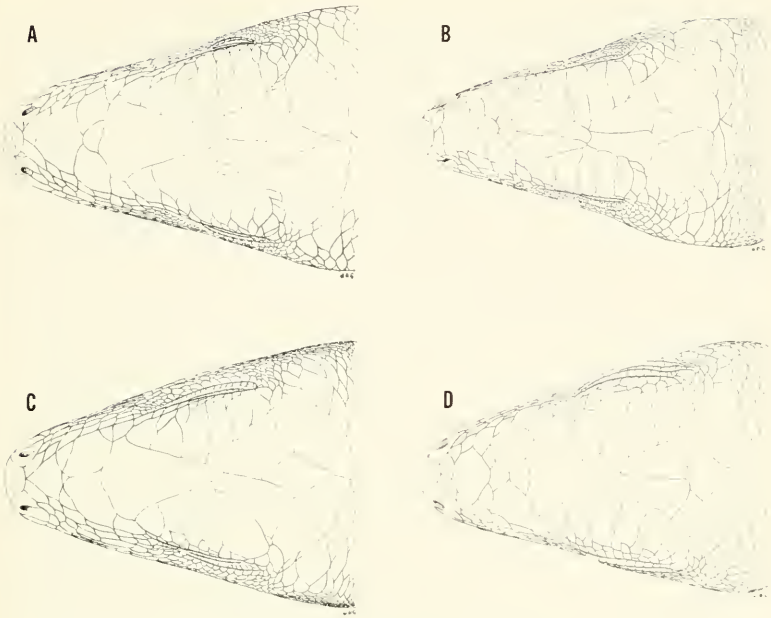

Figure 3. Dorsal view of the head of 4 specimens of *Sphenomorphus taylori*. A) Holotype, American Museum of Natural History 42018 from "Bougainville." B) Museum of Comparative Zoology 65857 from Kieta area. C) Paratype, American Museum of Natural History 42016 from "Bougainville." D) Museum of Comparative Zoology 78090 from Aresi area (2500 feet).

S. fragosus. *S. concinnatus* from Mutahi (2200-3200 feet), for example, are as dark dorsally as *S. fragosus*, whereas *S. concinnatus* from many lowland areas of Bougainville, as well as the small off-shore islands, are generally a much lighter golden brown dorsally.

The highland *S. concinnatus* also tend to show a middorsal series of dark brown to black blotches somewhat similar to those of *S. fragosus*. In addition there is a diffuse series of small dark blotches along the dorsolateral line of highland *S. concinnatus* which is generally lacking or is much less well defined in the populations from the lowlands of Bougainville and the off-shore islands. Each of these dark blotches along the dorsolateral line of highland *S. concinnatus* is often associated with a small whitish spot situated anterior to and just above the dark blotch.

This dorsolateral series of dark and light blotches in *S. concinnatus* is rather similar to the continuous, dark dorsolateral line with its associated light line in *S. fragosus*. One might think of the *S. fragosus* pattern as originating from the fusion (into a continuous line) of the distinct blotches in *S. concinnatus,* or, vice versa, the formation of the distinct blotches in *S. concinnatus* from the fragmentation of the continuous line in *S. fragosus*.

S. concinnatus differs rather strikingly from *S. fragosus* in displaying a large black spot between the external ear opening and the point of insertion of the forelimb. This black spot is totally lacking in *S. fragosus*. Furthermore, in life, *S. concinnatus* lacks the yellow ventral coloring of *S. fragosus*.

Juvenile and young adult *S. taylori* are quite unlike either of the species' two Bougainville relatives in displaying a color pattern of light transverse bars on the dark brown mid-dorsum. The flanks are a lighter grayish brown to beige with faint white spots which may coalesce to form distinct vertical light lines. In large adults all indications of the transverse and vertical bars may have vanished.

OSTEOLOGICAL COMPARISONS WITH BOUGAINVILLE RELATIVES

Single skulls have been prepared of *S. fragosus, S. concinnatus* and *S. taylori*.

Those features of the skull osteology that are characteristic of the *variegatus* species group to which the three species belong (see Diagnosis) are as follows: skull fairly deep throughout much of its length; 9 teeth on the premaxillae; palatine bones and palatal rami of the pterygoid bones meet along the midline to form an extensive secondary palate; no ectopterygoid process to the palatine which would exclude the palatal ramus of the pterygoid from a position on the infraorbital vacuity; postorbital bone lacking; supratemporal fenestra small or absent, in the latter case being obliterated by the backward extension of the postfrontal between the squamosal and parietal bones.

Differences between the skulls of *S. fragosus, S. concinnatus* and *S. taylori* are minor except for the shape of the teeth on the anterior part of the maxillae and dentaries in *S. taylori*. In this species the anterior maxillary and dentary teeth are slightly pointed and curved posteriorly, whereas the corresponding teeth in *S. fragosus* and *S. concinnatus,* as well as in other members of the *variegatus* species group that have been examined, are straighter and more peg-like.

The more pointed anterior maxillary and dentary teeth of *S. taylori* may be indicative of a shift to slightly more predaceous habits than either of its two Bougainville relatives.

S. taylori also differs from both *S. concinnatus* and *S. fragosus* in that the frontal bone forms a surface suture with the maxilla to separate the prefrontal and nasal bones, whereas in *S. concinnatus* and *S. fragosus* the prefrontal makes contact with the nasal through a finger-like anterior projection.

ECOLOGICAL COMPARISONS WITH RELATIVES ON BOUGAINVILLE

Of the three species of the *variegatus* species group on Bougainville, very little is known about the ecology and habits of *S. taylori* or *S. fragosus*. The ecology and habits of *S. concinnatus* are, however, somewhat better known.

S. concinnatus is a common species on Bougainville from the coast to about 4000 feet, although it is occasionally found to an altitude of at least 5000 feet. The species inhabits dense primary forest and shows a marked preference for moisture. Although normally crepuscular, it is found in the open by day during rain and on damp overcast days. Only very rarely are individuals seen basking in small patches of weak sun. The species is not a burrower but lives in leaf litter on the forest floor.

S. taylori is almost certainly a montane species, having been collected between 1600-3000 feet. Native collectors have obtained all the MCZ specimens, and where collectors could recall, the specimens were found under and beside decayed logs on the forest floor. The species does not seem to be a true burrower, however.

S. fragosus has been collected between 4000-4300 feet in the central highlands of Bougainville. The specimens were under moss and fallen *Pandanus* leaves on the ground in fairly open areas. None were found out in the open in spite of the fact that both days on which the species was collected were dull and overcast.

S. concinnatus is by far the most widespread and numerous of the three species of the *variegatus* species group on Bougainville. It is the only species of the three known to occur in the lowlands, where it is very common, and it extends through the known altitudinal range of its two relatives (1600-4300 feet) to an elevation of at least 5000 feet. Furthermore, *S. concinnatus* is the only one of the three species known to occur sympatrically with the other two. *S. fragosus* and *S. taylori* have never been found in the same area, although, admittedly, this may be a result of sampling error in populations of low density.

Although only the low and middle (0-5000 feet) elevations of Bougainville have been adequately collected, it would appear that *S. fragosus* and *S. taylori* do, in fact, occur in less dense populations than other Bougainville skinks (e.g., *S. concinnatus, S. solomonis* and *S. tanneri*) at these elevations. Thousands of reptiles and amphibians have been obtained by Parker and his collectors in all kinds of accessible habitats on Bougainville, and it is unlikely that animals as large or larger than these abundant skinks should not come to light in numbers approximately proportional to their relative frequency in the whole fauna.

The possibility can not be excluded, however, that *S. fragosus* and *S. taylori* may occur in very peculiar habitats that were not widely sampled during the general collecting, or that both species occur in much higher population densities at elevations above those collected.

Nothing is known of the mode of reproduction of *S. fragosus* or *S. taylori,* although *S. concinnatus* is live-bearing. Thirty gravid *S. concinnatus* from Kunua, Bougainville, contained 1-3 oviducal eggs or embryos in various stages of development. The snout-vent lengths of these 30 females ranged from 54-64 mm, and all were collected in the period May-June.

EVOLUTIONARY HISTORY OF THE SKINKS OF THE *VARIEGATUS* SPECIES GROUP ON BOUGAINVILLE

Within the *variegatus* species group, *S. concinnatus, S. fragosus* and *S. taylori* are most likely each other's closest living relatives.

S. concinnatus and *S. fragosus* are more similar to each other in overall external morphology, skull osteology, and color pattern than is any other skink of the *variegatus* species group to either one of them. Furthermore, the fact that two such similar species occur together on Bougainville and not one on Bougainville and the other on Celebes, for example, lends support to the hypothesis of their close relationship.

If it can be admitted that within the *variegatus* species group the fragmentation of the head scales as in *S. fragosus* is a specialization and the low supraocular number (4 as opposed to the more usual 5 or more) of *S. concinnatus* is primitive, then an animal similar to *S. concinnatus* can easily be conceived of as being ancestral to *S. fragosus.*

The evidence for the close relationship between *S. fragosus* and *S. taylori* rests primarily on the peculiar fragmentation of many corresponding head scales. The fact that among skinks this fragmentation is unique to two species of the same species group on the

same small island minimizes the possibility of convergence as an explanation.

The large body size, the high number of midbody scales, and the slightly pointed anterior maxillary and dentary teeth of *S. taylori* must again be viewed as specializations for the *variegatus* species group, derivable, perhaps, from a stock similar to present-day *S. fragosus*.

The structural changes in the evolution of the three species of the *variegatus* species group presently known from the Solomons may have proceeded along the general lines suggested by the sequence of living species: *S. concinnatus* → *S. fragosus* → *S. taylori*.

The ancestor of these three living species would have undoubtedly been recognized as an *Otosaurus* or *Parotosaurus* by Boulenger (1887), Smith (1937) or Mittleman (1952) and simply as a member of the *variegatus* species group by us. This ancestor most likely arrived in the Solomons from New Guinea or the Bismarck Archipelago, as the *variegatus* species group is unknown from Australia or the islands to the north, east or south of the Solomons.

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Mrs. Patricia H. Kerfoot and Mr. Joshua B. Clark executed the line drawings of *Sphenomorphus fragosus* (Fig. 1) and *S. taylori* (Fig. 3), respectively.

Dr. Ernest E. Williams of the Museum of Comparative Zoology has read the paper in many prenatal drafts and has, as usual, offered numerous helpful criticisms.

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(Received 23 May 1967.)

TABLE 1

Morphological comparisons between *Sphenomorphus fragosus* and the 2 members of its species group on Bougainville.

	fragosus	*concinnatus*	*taylori*
Snout-vent length	31-73 mm	26-70 mm	59-160 mm
Scales around midbody	42-46	38-46	53-60
Number of supraoculars (touching frontal)	5 (3)	4 (2)	5-7 (3)
Supralabials below orbit	5th and 6th, less often just 6th	5th, rarely 6th	6th - 9th, although variable
Subdigital lamellae (4th toe)	18-21	18-27, usually 19-23	27-35
Nuchal scales	None	None	1-2 pairs, ill-defined

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THE *NOTATUS* GROUP OF *SPHAERODACTYLUS* (SAURIA, GEKKONIDAE) IN HISPANIOLA

Benjamin Shreve

INTRODUCTION

Some years ago while identifying *Sphaerodactylus* from Hispaniola, it came to my attention that several different forms had been allocated to *"Sphaerodactylus difficilis,"* or *"Sphaerodactylus notatus difficilis"* and that this nominal species was a veritable waste basket for any species (or subspecies) showing any resemblance to it at all. I therefore tried to see what could be done to clear up this puzzle. It was soon seen that related forms occurred outside of the region. However, in order that a beginning could be made, and so that the whole undertaking would not get out of hand, I decided to confine my study to the *notatus* group on the island of Hispaniola (and its nearby smaller islands). Extralimital forms were indeed studied to gain an idea of the status of the forms revised, but no extralimital forms were themselves reviewed, though references to them will be found in the text.

Thirteen taxa are discussed herein, including not only forms obviously close to *notatus* but also those less closely related but formerly confused with *notatus* relatives.

METHODS

A number of scale counts are employed here which have not previously been commonly used in this genus. The dorsal scales are counted on a line from the rear of hind limb to the front of fore limb. This count is made just to one side of the vertebral line. Another scale count is made around the body at midbody. Midbody is taken as the point midway between the rear limit of the insertion of the fore limbs and the forward limit of the insertion of the hind limbs. The standard distance, as used here, is about

the same as previous usage for this term; i.e., the distance between the end of the snout and the middle of the eye is projected on the dorsum, equally distant from the rearward limit of the fore limbs and the forward limit of the insertion of the hind limbs, respectively. Again, a position just alongside the vertebral line is taken for this longitudinal count.

The lamellae under the fourth toe are counted from the first lamella at the separation of the digit, up to, but not including, the terminal "disk." Either right or left foot is used for this count, depending on the suitability and position of the fourth toe for the count. Sometimes, when doubt has existed, both sides have been counted.

The phrase "scapular spot," as used here, applies to the dark marking often present on the back in the shoulder region, with frequently one or two white spots within it or else white border markings, developed in varying degree.

ACKNOWLEDGMENTS

I am grateful to the following institutions which have loaned material for study and to the persons in charge of their collections. The abbreviation of each institution as used in the text follows the name: American Museum of Natural History (AMNH), Charles M. Bogert; United States National Museum (USNM), Doris M. Cochran and James A. Peters; Stanford University (SU), George S. Myers; British Museum of Natural History (BM), Miss Alice G. C. Grandison; Field Museum of Natural History (FMNH), Robert F. Inger; Carnegie Museum (CM), Neil D. Richmond; University of Florida (UF), Coleman C. Goin. For Museum of Comparative Zoology, the abbreviation MCZ is used. I also wish to extend my thanks to the National Science Foundation for the grants (NSF 16066 and GB 2444) that made this study possible.

SPHAERODACTYLUS NOTATUS DIFFICILIS Barbour

Sphaerodactylus difficilis Barbour, 1914: 265, Santiago de la Vega, San Domingo = La Vega, La Vega, Dominican Republic; Barbour, 1921: 241 (part); Mertens, 1939: 42 (part); Cochran, 1941: 115 (part).

Description. The supranasal scales are usually separated, the granular dorsal neck scales do not extend to the insertion of the fore limb. The ventral scales are not usually keeled at all, although the dorsals are, as in all members of the group. The scale counts

for 137 individuals are: (5) 6-9(10) scales in standard distance, going to 11 in subadult specimens, 28-43 dorsal scales between rear of hind limb and front of shoulder, 39-54 scales around the body at midbody, (9)10-13(14) lamellae under the fourth toe. In coloration the female has three longitudinal dorsal dark stripes on the head and neck, sometimes extending further, with varying amounts of spotting elsewhere dorsally. The male color shows dorsal spotting, frequently confined to the neck and anterior part of the back but also quite often extending onto the head and the rest of the back. Sometimes dorsal marking is practically obsolete. Below, spotting or darker washing is mostly confined to underside of head and throat but sometimes more extensive. The scapular spot present in females is frequently absent in the adult male coloration. The largest head and body measurement is 33 mm (MCZ 63184 and 63191, both females from Bombardopolis, Haiti).

Originally described as a full species, *difficilis* appears barely separable from *S. notatus* races (the type locality of typical *notatus* is Key West). In general, Cuban specimens seem to resemble those from Key West rather than those from the islands of the Great and Little Bahaman banks, although those from various localities in Cuba also show some geographical variation, the evaluation of which is beyond the scope of this work.

My own comparison of Key West examples and Cuban specimens[1] from various localities with what I consider *difficilis* shows a usually less stocky build in the latter. The middle head stripe of the female and immature coloration of *difficilis* usually narrows or stays about the same width as it proceeds posteriorly and has decidedly uneven edges, whereas in Key West and Cuban specimens this stripe is likely to have more even edges and widen as it extends posteriorly.

The scale counts of Cuban and Key West animals (6 of each) follow: 6-7 scales in standard distance, 26-30 dorsal scales between rear of hind limb and front of shoulder, 37-47 scales around the body at midbody, (8)10-13 lamellae under the 4th toe, the figure in parentheses representing one specimen. The

[1] In a recent work, Schwartz, 1966, recognized a number of races of Cuban and Bahaman *notatus*. Actually, the *notatus* specimens used are a composite of the races separated by Schwartz (1966). He confines typical *notatus* to Key West and part of the Florida mainland.

corresponding counts for 137 *difficilis* follow: (5)6-9(10) (reaching 11 in subadult examples), 28-43, 39-54, (9)10-13(14). As can be seen, the dorsal count between the rear of hind limb and front of shoulder shows the least overlap.

As just mentioned, there is considerable variation in the Hispaniolan population. It was at first thought that the population from Haiti and the northwestern part of the Dominican Republic was separable from the rest, on lower scale counts, but there is considerable overlap. In Puerto Plata, Sosua, and to a less extent in Sabana de la Mar specimens, there is a tendency for head streaks of the female to break up into spots. In those from the first two localities, there is a tendency for the scapular spot not to persist in the adult. As in most examples of this form, there are two white spots within the scapular spot. Los Bracitos females, the two specimens from near Peña (the latter subadult), and two of three females from Licey Almedio near Tamboril[1] (the third with obsolete scapular spot), show only one white spot there. In those from Los Bracitos the spot appears to represent the fusion of two spots. One of the two males from Pascal Island shows black spotting on a whitish head. The specimen from the unlikely locality of Paradis will be discussed below under *S. n. randi*.

At all events, the variation mentioned above does not seem to be sufficient or consistent enough, geographically, to warrant further division into races.

Material examined: HAITI. *Departement du Nord Ouest.* Bombardopolis: MCZ 63174-63217; Port de Paix: MCZ 63219-21. *Departement du Nord.* Cap Haitien: AMNH 50117, MCZ 63233; Grande Rivière: MCZ 9365-6; Ti Guinin near Cap Haitien: MCZ 66283. *Departement de L'Artibonite.* Hinche: BM 1948.1.4.27-30. DOMINICAN REPUBLIC. *Monte Cristi.* El Ahogado, near Monte Cristi: AMNH 42142-3; Monte Cristi (from houses): AMNH 41995-6; 1½ miles west of Monte Cristi: AMNH 42148-9, and five untagged specimens; small island in Monte Cristi Bay: AMNH 42140; Muertos Island, Siete Hermanos: USNM 76718-23. *Puerto Plata.* Puerto Plata: MCZ 5444 (paratype), AMNH 41340, 41975-7; Sosua: MCZ 13663, 43664-6, 44400, USNM 121521-2. *Samana.* Pascal Island, Bay of Samana: AMNH 41979-85; Sanchez: MCZ 44395-6. *Santiago.* Licey Almedio, near Tamboril: MCZ 78732-5; 3 km south of Peña: MCZ 57822-3.

[1] Tamboril is apparently a different name for the locality referred to above as Peña.

La Vega. La Vega: MCZ 7834-5 (type and paratype). *Duarte.* Los Bracitos: AMNH 45201-2, 45204, 45206-7, 45209-12, 45214-5, 45217-20. *Seibo.* Sabana de la Mar: AMNH 41992-3, 50047, 50122-4, 50232, MCZ 57824-6, 57831-3. *Barahona.* Paradis: AMNH 51466. *Distrito Nacional.* Santo Domingo City: SU 14694. *San Pedro de Macoris.* 31 mi. east of Santo Domingo City: AMNH 49990-2.

Field notes. Through the courtesy of Miss Alice G. C. Grandison, the following color note has been supplied for the series from Hinche by the collector, Ivan Sanderson: "Upper surfaces fawn brown, prominently spotted with jet black. Spots tend to run into three lines on head, while on shoulders are a pair of well defined jet black spots bordered by an intense white point on either side. Underside of head and forebody pale gray and semi-transparent. Of limbs, lower belly and tail, same, but minutely speckled with black."

Identification aids. The three dorsal streaks in the female and immature coloration will serve to distinguish this form from all other Hispaniolan members of this group. Outside of its own races, probably most closely related to *S. b. brevirostratus,* so see identification aids for this form (p. 00).

The following form is named for A. Stanley Rand, co-collector of the type series and student of West Indian herpetology.

Sphaerodactylus notatus randi subsp. nov.

Holotype: MCZ 57839, female, from Oviedo, Pedernales, Dominican Republic, collected by Clayton E. Ray and A. Stanley Rand, August 20, 1958.

Paratypes: MCZ 57840-5, with the same data as the type; MCZ 57838, also with the same data as the type, except that the collecting date is August 19, 1958.

Diagnosis. The new form differs from *S. notatus difficilis* in apparently slightly higher scale counts as follows (the count of the type followed by those of the paratypes in parentheses); standard distance 8 (7-10); dorsal scales from rear of hind limb to front of shoulder 44 (36-40); around body at midbody 54 (48-52); lamellae under 4th toe 12 (12-13); also, *randi* appears to not grow quite as large as *difficilis.* In the female coloration there is no sign of the three head and nuchal stripes of typical *difficilis;* instead, above, there is much spotting, marking, and washing of a light brown ground color with dark brown; back of head showing ground color more than is shown elsewhere, a poorly developed

scapular spot, a dark brown marking preceded by a curved whitish transverse streak, convexly directed anteriorly, followed by a dark spot, marked posteriorly by whitish; below, ground color about the same as above, stippled and washed with dark brown.

Most of the paratypes, above, show the same kind of markings as the type. However, the scapular spot is practically obsolete in some, and in only one, a male, takes the form of a black spot entirely borderd with whitish, which may represent the maximum in its development. There is also variation in the spotting, particularly on the head and neck. Whitish spots and markings are present in some. Two show a faint marking on the back of the head and neck, somewhat reminiscent of that of *S. b. brevirostratus,* described below. Below, the markings are like those of the type, except that they are stronger in some.

Of the four male paratypes, two apparently have not lost the female or immature coloration. The two showing what is apparently the adult male coloration, above, have lost much of the dorsal markings, the head being whitish with dark brown or black spots above and below, including throat; otherwise, below, marked similarly to the rest of the type series. Even the males with the female or immature pattern are decidedly spotted under the head and on the throat. The females show little of this.

The male coloration of *difficilis* somewhat resembles the female coloration of *randi,* although it usually shows less dense markings. However, some males of *difficilis* resemble those of *randi.*

Measurements (in mm). Type, MCZ 57839: length, head and body, 29; length of tail, 26. Largest paratype, MCZ 57840: head and body, 27; tail regenerated.

Remarks. It might be supposed that this form is the representative of *difficilis* in the Barahona Peninsula, but a specimen from Paradis (Paraiso) appears to be a male *difficilis.* It has the reduced spotting characteristic of a male of that form, especially reduced on the head, with the scale counts being a bit low for *randi* although barely within the limits of that form, except for the rear of hind limb to front of shoulder count which is one below the limit for *randi.* Also, the head and body length is one millimeter more than the maximum for *randi.* The counts for this specimen, AMNH 51466, are: standard distance 8, dorsal scales between rear of hind limb to front of shoulder 35, around midbody 48, lamellae under 4th toe 12. It is possible that the locality data for this animal may be incorrect.

Identification aids. This has essentially the scale characters of *S. n. difficilis* but differs in counts and color, as stated in the diagnosis.

Another race of *notatus,* described below, is named for Jay M. Savage because of his interest in this group.

SPHAERODACTYLUS NOTATUS SAVAGEI subsp. nov.

Sphaerodactylus difficilis: Grant, 1952: 187; 1956: 86; Savage, 1954: 328.

Holotype: SU 14695, a female, from La Romana, Altagracia, Dominican Republic, collected by Chapman Grant in December 1946.

Paratypes: SU 14696-708, with the same data as the type; MCZ 73900 from the same place, collected by Clayton E. Ray and Robert R. Allen, March 27, 1963.

Diagnosis. Apparently most closely related to *S. notatus difficilis* from which it differs in having larger scales, or at least lower scale counts, although there is considerable overlap. The scale counts follow, with those of the paratypes in parentheses: scales in standard distance 6 (6-7 and up to 8 in the immature); dorsal scales between rear of hind limb and front of shoulder 28 (27-34); scales around body at midbody 42 (36-44); lamellae under 4th toe 13 (11-14); and the limited extent of the male escutcheon, this not extending onto the leg. There is also a difference in color. The female coloration shows but little evidence of the head stripes of *difficilis,* only a rough tendency for the spots to form into lines, most notably the ones behind the eye. Males would appear to average more heavily spotted than those of *difficilis.* Subadult specimens, presumably of both sexes, instead of being spotted show a series of cross bars across the back, with two stripes extending back from each eye and joining on the back of the head in somewhat the same manner as in typical *brevirostratus* (to be described), the central stripe being mostly obsolete. Subadults also have an ill-defined scapular spot, the foremost dark band on the neck being followed by two whitish spots, this band being more conspicuous than those following. The scapular spot appears to disappear as the animal gets older, especially so in the male, but is entirely absent in the female type.

Measurements (in mm). Type, SU 14695: length, head and body, 32; length, tail, 26 (apparently regenerated). Largest paratype, SU 14696: head and body, 30; tail missing.

Identification aids. This is one of the two forms where the male escutcheon does not extend onto the leg. The other is *S. n. juanilloensis.* This, as far as known, is a character unique within the Haitian *notatus* group. Beyond this the racial diagnosis is covered under each form.

SPHAERODACTYLUS NOTATUS JUANILLOENSIS subsp. nov.

Holotype: MCZ 73901, a female, from Juanillo, Altagracia, Dominican Republic, collected by Clayton E. Ray and Robert R. Allen, March 29, 1963.

Paratypes: MCZ 73893-98, UF 21970-75, with the same data as the type. MCZ 73899, Dominican Republic, Altagracia, 1 km north of Boca de Yuma, collected by Clayton E. Ray and Robert R. Allen, March 27, 1963.

Diagnosis. Apparently most closely related to *S. notatus savagei* from which it differs in coloration. The coloration, notably the female and immature, resembles that of the immature *savagei.* It differs particularly in that the dorsal cross bands are arranged in pairs, the two bars of the pair separated by a narrow white area; the scapular spot in the female well developed, squarish, with two white spots in the middle, located as usual betwen the shoulders. In the male coloration there is also a tendency for the dark spots to form indistinct bars or at least to coalesce. In adults of both sexes of *savagei* there appears to be no tendency toward bar formation. The scale counts for *juanilloensis* follow, with those of the paratypes in parentheses: scales in standard distance 6 (5-7, one with 8, scale abnormality present, evidently scar tissue); dorsal scales between rear of hind limb and front of shoulder 29 (25-32); scales around the body at midbody 42 (40-48); lamellae under 4th toe 12 (12-14).

Measurements (in mm). Type, MCZ 73901: length, head and body, 26; part of tail missing. Largest paratype, UF 21972: head and body, 31, a female; tail missing.

Identification aids. See *S. n. savagei.*

The following form is named for James D. Lazell, Jr., the co-collector of the type specimen and other valuable herpetological material.

SPHAERODACTYLUS LAZELLI sp. nov.

Holotype: MCZ 63218, a male, from Cap Haitien (under bark of tree in shady gully), Departement du Nord, Haiti, collected by A. Stanley Rand and James D. Lazell, Jr., July 16, 1960.

Diagnosis. Possibly most closely allied to *S. notatus difficilis* with which it is sympatric, differing in lower scale count from rear of hind limb to front of shoulder, in having distinctly keeled scales on the throat, and in coloration, with a very prominent scapular spot and two black spots preceding it (female coloration unknown).

Description. Snout long, rather pointed, distance of eye from tip of snout greater than distance of eye to ear; rostral with median groove; nostril between rostral, first supralabial, a larger supranasal and three smaller scales, the third or lowest particularly small; supranasals separated by one scale; three large and one small supralabial to below center of eye, or a bit beyond; head above and on sides covered with small juxtaposed keeled scales, those on snout slightly enlarged; scales on back enlarged, somewhat elongate, keeled and subimbricate; the more granular scales of the neck appear well anterior to the forward level of the shoulder; 5 scales in standard distance; 25 dorsal scales between rear of hind limb and front of shoulder; 42 scales around the body at midbody; 11 lamellae under the 4th toe; mental somewhat larger than rostral; two large infralabials, followed by a small one, to center of eye; two enlarged squarish chin shields behind mental; behind scutes just mentioned, scales decreasing in size posteriorly to throat, increasing in size on throat and chest, and again on belly, smooth, except keeled on throat and forward up to chin shields; tail above with scales like dorsum but smaller; below, with scales like belly at base, but beyond, those on midline enlarged, especially nearer terminus (tail apparently regenerated, possibly twice).

Coloration in alcohol. Above, light brown, a large diamond-shaped scapular spot about on a level with the anterior border of the shoulders, with a white spot near each lateral corner. Preceding this are two prominent black or dark brown spots, both on the midline, one on the neck and the other on the occipital region of the head; an indistinct, dark brown streak from the rear of the supraocular region, on each side, to the anterior edge of the neck spot, another from each eye along the side of the head on to the neck. The body, limbs and tail are lightly spotted with black or dark brown, three spots just to the rear of the scapular spot being particularly prominent. There is a whitish chevron-shaped bar, with the apex directed rearward, a bit posterior to the base of the tail; a narrow crossbar of the same color on the tibia. Below, washed with dark brown, especially nearer the sides;

also lightly spotted with dark brown nearer side of throat and chest.

Measurements (in mm). Type, MCZ 63218: length, head and body, 31; length, tail, 29 (apparently regenerated).

Identification aids. The keeled throat scales will serve to separate this from all forms which have only smooth scales ventrally. From those that have keeled throat scales, the very large scapular spot and the two spots preceding it are a type of coloration not seen elsewhere in this group. However, the female of this form is not known. The dorsal scale count from the rear of hind limb to the front of the shoulder is lower than that of any other form, although with more material this might be found to overlap with *S. b. enriquilloensis*, a form with slightly keeled throat scales, in this character.

Sphaerodactylus brevirostratus brevirostratus

sp. and subsp. nov.

Sphaerodactylus difficilis: Barbour, 1921: 241 (part); Cochran, 1941: 115 (part).

Holotype: MCZ 63234, a female, 5 km south of Dufort, south of Leogane, Departement de l'Ouest, Haiti, collected by A. Stanley Rand and James D. Lazell, Jr., July 31, 1960.

Paratypes: All from HAITI. *Departement de L'Artibonite.* Saint Marc: AMNH 49680, William G. Hassler, April 1935. *Departement de l'Ouest.* With the same data as the type: MCZ 63235-8; Boutillier Road near quarry: MCZ 64514, Ernest E. Williams and A. Stanley Rand, August 15, 1959; west of Carrefour: USNM 117307-8, Anthony Curtiss, May 11 and 15, 1943; Carrefour Feuille, Port-au-Prince: MCZ 64812-3, Ernest E. Williams and A. Stanley Rand, August 15, 1959; Damiens: AMNH 50120-1, William G. Hassler, May 2, 1935; Diquini: MCZ 64815-21, Luc Whiteman, March 10-11, 1961; Eaux Gaillées: MCZ 51315-6, Anthony Curtiss, April 22, 1950; "Ferronai": MCZ 13458, Glover M. Allen, August 1919; Furcy: USNM 124158, Anthony Curtiss, June 1944; Glore: USNM 118908-14, Anthony Curtiss, May 18, 1943; Hatte Latham: AMNH 90168-9, USNM 117151, Anthony Curtiss, December 7, 1946, and February 13, 1943; La Fond near Jacmel: MCZ 64822, Luc Whiteman, April 20, 1961; Manneville: MCZ 64804-11, Ernest E. Williams and A. Stanley Rand, August 13-14, 1959, CM 38882, George Whiteman, 1963, BM 1948.1.4.31-33, Ivan Sanderson, January

23, 1937; Mon Repos: USNM 69124, Gerrit S. Miller, Jr., March 5, 1925; Petionville: USNM 59185, Paul Bartsch and J. B. Henderson, April 1, 1917; Pont Beudet: BM 1948.1.4.34, July 12, 1937; 8 miles north of Port-au-Prince (fig tree in cotton field): AMNH 49588, 49590-1, William G. Hassler, April 18, 1935; Port-au-Prince: USNM 118867-70, Anthony Curtiss, USNM 59179 Paul Bartsch and J. B. Henderson, April 24, 1917, SU 14688-14693, Major Chapman Grant, December 18, 1941; Source Puantes: USNM 117159-64, Anthony Curtiss, November 18, 1943; Trou Caiman: USNM 117153-6, Anthony Curtiss, January 16, 1943; Trou Forban: USNM 117157-8, 118894, Anthony Curtiss, October 1942.

The locality "Ferronai" has not been located on the map, but has been listed under Departement de l'Ouest, as this seemed a likely place of origin, the majority of the localities being from there. Through the courtesy of Mrs. W. E. Schevill, I was able to examine the field journal of the collector, the late Glover M. Allen. The locality was not mentioned.

Diagnosis. Possibly most closely allied to *S. nicholsi* Grant from which the new form differs in having smaller scales (average larger scale counts), larger size, less short and blunt snout, and different coloration. Also related to, and in the past confused with, *S. notatus difficilis,* from which the new form differs in its smaller size, shorter and more blunt snout, more stocky build, in having larger scales (smaller average scale counts) and in coloration.

Description. (Paratype variation in parentheses.) Snout short, blunt; distance of eye from tip of snout slightly greater than distance of eye to ear; rostral with median groove; nostril between rostral, first supralabial, a large supranasal and two smaller scales; supranasals separated by one scale (in some, separated by two or more scales); three large and one small supralabial to below center of eye, head above and on sides covered with small juxtaposed keeled scales, those on snout enlarged; scales on back enlarged, elongate, keeled and subimbricate; the more granular scales of the neck appear anterior to the forward level of the shoulder (also in paratypes); 6 scales in standard distance (6-7 in adults, subadults going to 8); 31 dorsal scales between rear of hind limb and front of shoulder (28-35, and one example 38, with scale abnormality in the sacral region); 41 scales around the body at midbody (37-45); 10 lamellae under the fourth toe (9-12, only two instances of the last figure); mental somewhat larger than rostral; two large infralabials followed by a small one

to center of eye; three small squarish chin shields behind mental; behind these the scales decreasing in size, posteriorly, to throat, increasing in size on throat and chest and again on belly, smooth (a very few throat scales very slightly keeled in a few of the paratypes); tail, above, with scales like dorsum but smaller and more imbricate and not keeled near terminus; tail, below, with scales like those of belly.

Coloration in alcohol. Above, ground color light grayish brown; on head a dark brown streak extending from end of rostral, where it is joined with its fellow on the other side of the head, the color on rostral being rather dark gray, extending through eye to back of head where it again joins its fellow, this time in a figure which resembles the top of a heart with the direction of the possible apex toward the snout. Within the area enclosed by these markings and to some extent just outside, the ground color becomes very pale; also several dark brown spots inside of this area, one behind eye and joining onto eyelid on each side, two others more or less between eyes and one on snout. Behind the top of heart-like figure on the back of the head is a second one, very similar to, but less well defined, and more or less joining the first and just behind it, both with a more or less distinct whitish border on the inner posterior margin. A distinct scapular spot consisting of an almost transversely oval blotch of black with a small white spot on each side near its lateral edge; just preceding the scapular spot is a thin, rearwardly curved, whitish, transverse line; elsewhere, back spotted with dark brown; the limbs spotted with the same, including white markings on the hind limbs; an obscure whitish streak at posterior side of body; a white streak bordered with dark brown along side of tail going on to rear of thigh; tail above spotted and marked with dark brown and white spots, no special marking at root of tail.

Below, whitish; longitudinal dark brown lines on venter, becoming more broken under head and neck.

In the female paratypes the head markings may be less heart-shaped, less well defined or broken, the hinder one sometimes being obscure or absent. Sometimes the head spots inside are reduced or absent or united with each other and the enclosing streaks in various ways.

In the males the head markings may be even more reduced or faint and in some are entirely absent, being replaced by small spots. In the males the scapular spot, although sometimes nearly obsolete, is very persistent; yet, USNM 117157, a female, is the

only one which shows no trace of it. The paratypes from Trou Forban and Source Puantes, however, often show less development of the scapular spot than those from elsewhere.

Other variations are the reduction to almost total absence of the ventral markings in some specimens, and the variation in shape of the scapular spot which is sometimes more square or longitudinally elongate than in the type.

Measurements (in mm). Type, MCZ 63264: length, head and body, 22; length, tail, 20. Largest paratype (one) MCZ 64805: head and body, 26; tail, 27.

Remarks. In order that a comparison may be made with the scale counts of the new form, counts for *nicholsi* are supplied in the same order as they occur in the description: standard distance 6-7 (two adults and one subadult 7); rear of hind limb to front of shoulder 25-32; around body at midbody 35-40; lamellae under fourth toe 9-12 (two examples at 12). These counts were based on 18 *nicholsi.*

Some of the type series were found in leaf litter on the ground, while specimens AMNH 49588, 49590-1, from 8 miles north of Port-au-Prince, were collected on a fig tree in a cotton field.

S. n. difficilis is not known to occur with this new form anywhere.

Field notes. Through the kindness of Miss Alice G. C. Grandison, the following field notes have been supplied for the British Museum specimens collected by Ivan Sanderson: The three from Manneville were collected among leaves under thorns. The color was described as ". . . brown lighter to almost white below. Tail small, yellowish. Throat spotted with black. spots run in lines on belly. Flanks and dorsum likewise spotted, tending to run in lines on flanks." The Pont Beudet specimen was collected in a small mud house. The color was described as fawn, tail unspotted, head with black reticulum.

Identification aids. The usually prominent, dark, longitudinal, ventral streaks will serve to distinguish this form from all others in the present group, except the race to be described next, *enriquilloensis.* However, in some specimens these are not entirely evident. The latter form, however, differs in having a decided suppression of the dorsal pattern including absence of the scapular spot, which is almost always present in both sexes of the typical form. Also, *enriquilloensis* has keeled throat scales, atlhough less strongly keeled than other forms covered in this work. *S. b. brevirostratus* belongs to the stocky, small, blunt-snouted group which includes,

aside from the race mentioned above, *noblei* and *darlingtoni* about to be described as new also. *S. armstrongi* Noble and Hassler may possibly also belong to this group. The separation from *S. n. difficilis,* with which it was formerly confused, is covered in the diagnosis.

SPHAERODACTYLUS BREVIROSTRATUS ENRIQUILLOENSIS subsp. nov.

Holotype: MCZ 57846, a male, from 4 km east of La Descubierta, near Lake Enriquillo, Independencia, Dominican Republic, collected by Clayton E. Ray and A. Stanley Rand, August 22, 1958.

Paratypes: All from the DOMINICAN REPUBLIC. *Independencia.* With the same data as the type: MCZ 57847-8; La Descubierta: AMNH 45125, G. K. Noble, September 25, 1922; Las Baitoas, Lake Enriquillo: AMNH 50153-63, William G. Hassler, August 5, 1935, AMNH 50205-09, William G. Hassler, August 5-8, 1935. *Barahona.* Barahona: AMNH 50118, William G. Hassler, June 23, 1935.

Diagnosis. This new form differs from the nominate subspecies in less blunt snout (overlap in this character), average larger scale counts as follows, the count of the type followed by those of the paratypes in parentheses: standard distance 7 (6-8), rear of hind limb to front of shoulder 31 (32-37), around body at midbody 46 (40-47), lamellae under fourth toe 10 (9-10, with one specimen at 11), and general reduction of the color pattern (in alcohol). There is also more keeling of throat scales than in the typical form. In the males, female head pattern virtually non-existent, sometimes heavily spotted, especially above, or virtually unmarked. The type is much spotted above, and below, on the head and throat, also showing evidence of the ventral lines of the typical form. In general these seem less developed in *enriquilloensis* than in *brevirostratus.* The female often lacks the head markings and, when present, there is only a rather indistinct replica of those of the typical form. Females may be virtually unmarked. Both sexes lack any scapular spot.

Measurements (in mm). Type, MCZ 57846: length, head and body, 23; tail missing. Largest paratypes, AMNH 50209, female, and AMNH 50118, male: head and body, 26; 50209 tail regenerated, 50118 tail missing.

Remarks. A specimen of *Sphaerodactylus notatus difficilis,* already referred to, from Paradis (Paraiso), seems to be the nearest approach to sympatry between that taxon and *brevirostatus.* The

locality is, however, *south* of that of the nearest *b. enriquilloensis* (Barahona) on the Barahona peninsula, well south of the Cul de Sac Plain. No other *difficilis* is known from the "south island," and the record may be an error of locality labelling.

Identification aids. As stated under the nominate form, this is one of those with keeled throat scales. This character, and the presence of longitudinal ventral streaks and suppression of dorsal color pattern, will serve to distinguish it from the other forms.

The following species is named for Dr. P. J. Darlington, Jr., the collector and the major student of West Indian zoogeography.

Sphaerodactylus darlingtoni sp. nov.

Sphaerodactylus difficilis: Cochran, 1941: 115 (part).

Holotype: MCZ 44380, a male, from Mt. Diego de Ocampo, summit dome, *ca.* 4000 feet, between Puerto Plata and Santiago, Dominican Republic, collected by P. J. Darlington, Jr., July 1938.

Paratype: MCZ 44379, with the same data as the type.

Diagnosis. Apparently most closely related to *S. noblei,* described below, differing in coloration and possibly slightly larger size, and also in the absence of distinctly keeled scales on the throat, in more lamellae under 4th toe, more dorsal scales from rear of hind limb to front of shoulder, and in having one small scale instead of two in contact with rear of nostril scale.

Description. (Paratype variation in parentheses.) Snout short, blunt; distance from eye to tip of snout about equal to that of eye to ear; rostral with median groove; nostril between first supralabial, a large supranasal and two smaller scales; supranasals separated by one scale; three large and one small supralabial to below center of eye (four and one on left side; small scale behind center of eye on right side, although the three and one formula mentioned for the type exists here); head above and on sides covered with small, juxtaposed, keeled scales, larger and mostly keeled on snout; scales on dorsum enlarged, elongate, keeled, and subimbricate; the more granular scales of the neck appear anterior to the forward level of the shoulder, the dorsals, however, decidedly smaller than those located more posteriorly, at the point just mentioned; scales in standard distance 7 (9); 45 dorsal scales between rear of hind limb and front of shoulder (43); 54 scales around the body at midbody (48) (in both type and paratype there is an incision at the side of the belly where it is suspected some scales may be missing, hence the two counts may be lower than they should

be); 12 lamellae under 4th toe; mental somewhat larger than rostral; two large infralabials followed by a small one to center of eye; two small squarish scales behind the mental (more irregularly shaped); somewhere behind the two just mentioned, scales decreasing in size posteriorly to throat, increasing in size on throat and chest and again on belly, smooth, unless it can be said some of the throat scales are very weakly keeled; base of tail, above, with scales like those of dorsum but more imbricate and slightly larger; posteriorly, scales abruptly smaller where regenerated; tail, below, with scales like those of belly but abruptly smaller under regenerated portion. It may be stated for the sake of clarity that both the type and the paratype have much of the tail regenerated.

Coloration in alcohol. Above, light brown, a very few dark brown spots on back and on head, particularly in loreal region; a blurred dark brown scapular spot; below, brownish white, a few obscure dark brown markings on throat and underside of head; the paratype, also a male, shows a persistence of what is probably the female and immature pattern; above, ground color slightly darker than that of type; a brownish black scapular spot, rather indistinct, with an obscure whitish line just preceding it and following a dark brown line from nostril to eye, emerging on the posterior side of eye and curving to meet its fellow from the opposite eye, forming a marking on the back of the head like that of *b. brevirostratus* and *noblei* but not shaped like the top of a heart; posterior lines just mentioned likely to be bordered with whitish and broken; inside the figure produced by the lines, dark and light mottlings and markings; elsewhere on back, a few, more than in type, small dark brown spots; below, brownish white, more or less powdered and marked with darker brown, a reticulate pattern of whitish and dark brown on underside of head and throat.

Measurements (in mm). Type, MCZ 44380: length, head and body, 26; tail regenerated. Paratype, MCZ 44379: head and body, 22; tail regenerated.

Identification aids. The very blunt snout, the absence of any ventral keeling, small size, and small scales are a combination of characters that will separate this species from all forms covered here.

The next species is named for the late G. K. Noble, the collector, whose work in Hispaniolan herpetology is especially important.

SPHAERODACTYLUS NOBLEI sp. nov.

Holotype: AMNH 45216, a male, from Los Bracitos, Duarte, Dominican Republic, collected by G. K. Noble, August 1929.

Paratypes: AMNH 45203, 45205, 45208, 45213, with the same data as the type.

Diagnosis. Allied to *S. notatus difficilis* Barbour from which the new form differs in more stocky build, smaller size, and coloration. Also allied to *S. b. brevirostratus* from which the new form differs in smaller scales or larger scale counts (slight overlap in longitudinal and standard distance counts), color, and seemingly smaller size.

The new form also differs from both in possessing distinctly keeled throat scales.

Description. (Paratype variation in parentheses.) Snout short, blunt; distance of eye from tip of snout slightly greater than distance of eye to ear; rostral with median groove; nostril between rostral, first supralabial, a large supranasal, and two smaller scales; supranasals separated by two scales (separated by one scale, at least one specimen giving the impression that the one scale has been made by the fusion of two); three large and one small supralabial to below center of eye; head above and on sides covered with small, juxtaposed, keeled scales, larger and mostly keeled on snout, scales on dorsum enlarged, elongate, keeled and subimbricate; the more granular scales of the neck appear anterior to the forward level of the shoulder, the dorsals, however, decidedly smaller than those located more posteriorly, at the point just mentioned; scales in standard distance 8(8-9); 35 dorsal scales between rear of hind limb and front of shoulder (35-38); 51 scales around the body at midbody (50-55); 11 lamellae under the 4th toe (9-11); mental somewhat larger than rostral; two large infralabials followed by a small one to center of eye; two small, rather irregularly shaped scales behind the mental; behind the two just mentioned, the scales decreasing in size posteriorly to throat, increasing in size on throat and chest and again on belly, smooth, except that the throat scales and to some extent those further forward, nearly to chin shields, are distinctly keeled; tail, above, with scales like those of dorsum, more imbricate, but about the same size or possibly slightly larger at the base, not keeled near terminus; below, with scales like those of belly.

Coloration in alcohol. Above, ground color brown, markings very similar to those of *S. b. brevirostratus* but less distinct, a dark brown line extending from nostril through eye and joining its fellow

in a marking which resembles the top of a heart with the direction of the apex toward the snout; within the area enclosed by the streaks just mentioned the ground color becomes pale, especially near the lines themselves; within this area a broken line proceeding backward from each eyelid on to the top of the head; other similar but obscure markings between the eyes and nearby and on the snout; a very indistinct suggestion of a second heart-shaped figure behind the first, with also a suggestion of lightening inside; on the neck an indistinct scapular spot consisting of a rather blurred dark brown spot preceded by a rather thin, rearwardly-curved, whitish, transverse line; elsewhere on back obscure dark brown spots with two very obscure whitish ones to the rear of two of the darker spots a bit behind the insertion of the forelimbs; an obscure whitish-bordered triangular spot at the base of the tail, the apex directed rearward; also obscure dark brown spots on the limbs and the rest of the tail, the latter rather densely spotted; a whitish dark brown bordered streak at the side of the base of the tail, extending on to rear of thigh; no whitish streak on side of body. Below, heavily dotted and dusted with brown, a line of small spots on the tail; throat and underside of head with a prominent black or dark brown and white reticulate pattern. Paratypic variation seems not extensive and sexual dichromatism seems to be very slight, if it exists at all, the single female paratype showing a fainter development of the pattern on throat and underside of head; otherwise all paratypes seem to be more obscurely marked above than the type, although one animal (not the female) shows two irregular white spots near the posterior edge of the indistinct scapular spot. Below, the only important difference, except that mentioned above, would be no line of spots under the tail (only two with tails, one detached).

Measurements (in mm). Type, AMNH 45216: length, head and body, 22; length, tail, 23. Largest paratype, AMNH 45213, a male: head and body, 24; tail missing.

Remarks. The following specimens, also from the Dominican Republic, tentatively referred to *noblei,* are not listed as paratypes. Boca del Infierno: USNM 74974-77, Gerrit S. Miller, Jr., February 28, 1928; Rio San Juan, Samana Peninsula: USNM 74943, Gerrit S. Miller, Jr., March 1928, but identified by Miss D. M. Cochran as *S. difficilis* (1941:115). These animals may belong to a distinct race. Thus the dorsal count from the rear of hind limb to the front of shoulder is 38-41 in the USNM examples above, whereas the count is 35-38 in the type series. The complete

counts, given in the same order, are: 7-9 (10 for one immature), 38-41, 50-56, 9-11. Three of the former have this count of 38, although only one of the latter has that figure. The type series has all but one paratype with only one scale separating the supranasals rather than two, although one other animal has a single scale in this position which has the appearance of two fused. All of the non-paratypic series have the supranasals separated by two scales. In view of the overlap in characters in the two series, taxonomic separation seems undesirable with such a small number of specimens. On the other hand, the possibility that with more material further separation would be desirable prevented the inclusion of these specimens as paratypes. It is believed, in any case, that the two series indeed are specifically identical, even if not subspecifically so.

The USNM non-paratypic specimens show weak or obsolete pattern on throat and underside of head, but they are regarded as females except for one doubtful male and a female equally doubtful.

Identification aids. The dark brown or black and white reticulation of the underside of the throat and head will separate this form from the others of the group, although in some individuals, as stated before, this pattern is weak or obsolete.

SPHAERODACTYLUS ARMSTRONGI Noble and Hassler

Sphaerodactylus armstrongi Noble and Hassler, 1933: 5, mountain top on property of G. Herrmann, near Paradis, Barahona, Dominican Republic, 2400 feet. Cochran, 1941: 119.

MCZ 57820-21 are referred here with some doubt, as they do not entirely fit the characters of *armstrongi*. Available for comparison is a paratype of *armstrongi* from the type locality. The two referred specimens differ from *armstrongi* in showing no keeled throat or chest scales, larger scales (smaller scale counts), and slightly different coloration: difference in the size and shape of the white scapular spots and the absence of the white streak near the back of the head in the male individual.

These two individuals may possibly be hybrids between *armstrongi* and *S. brevirostratus enriquilloensis* where the former meets the latter on descending to the lowlands. It is also possible that some other lowland form, such as *S. notatus randi,* could be involved, instead, but this is considered more unlikely. Another possibility is that these represent a lowland race or species.

Until more material can be examined, no conclusions about these specimens can be arrived at. The paratype (AMNH 51469) has the following counts: standard distance 8, dorsal scales from rear of hind limb to front of fore limb 46; scales around body at midbody 61; lamellae under fourth toe 10. The corresponding counts for MCZ 57820-1 are: 10, 42-43, 52, 10, the figure for 57821, on the last count, being doubtfully 10.

The type and paratype had head and body lengths of 27 and 28 mm, respectively (both male), while the two referred specimens, in numerical order, had 21 and 22 for the same measurement (male and female). The first two measurements are those of Noble and Hassler.

Material examined: All from the DOMINICAN REPUBLIC. *Barahona.* 5 kilometers south of Cabral: MCZ 57820-1; on mountain top on property of G. Herrmann, 2400 feet, near Paradis: AMNH 51469 (paratype).

Identification aids. The white scapular spots will separate *armstrongi* from all others in the Hispaniolan *notatus* group (female color unknown) except the two MCZ specimens discussed here.

SPHAERODACTYLUS ALTAVELENSIS Noble and Hassler

Sphaerodactylus altavelensis Noble and Hassler, 1933: 7, Alta Vela Island, Dominican Republic.

This form appears related to *S. notatus randi.* There is great similarity in color pattern, the main difference being a decidedly more definite arrangement of head markings in the female and immature coloration of *altavelensis.* Scale counts of the two forms are close, but those around the body appear to average higher in *altavelensis.* However, *altavelensis* has distinctly keeled throat scales, unkown in any race of *notatus.* This difference seems to me sufficient to maintain *altavelensis* as a full species. *S. notatus randi* appears to differ from *S. notatus difficilis* chiefly in coloration, the coloration in fact being more different between *randi* and *difficilis* than between the former and *altavelensis.*

The head and body length of MCZ 45947, a female paratype, is 29 mm, while Noble and Hassler give the length of the type of *altavelensis* as 26.5 mm, whereas the largest *randi* (the type) was 29 mm for this measurement. The scale counts follow: scales in standard distance 8-9; dorsal scales from rear of hind limb to front of fore limb 39-43; scales around body at midbody 54-56; lamellae under 4th toe 11-13.

Material examined: DOMINICAN REPUBLIC. *Pedernales.* Alta Vela Island: MCZ 45946-7 (paratypes).

Identification aids. The only form with keeled throat scales with which there is overlap in the scale counts (except standard distance) is *noblei.* The latter is distinguished by its blunt snout and distinctive ventral coloring and smaller size (see *noblei).*

The next form is named for William J. Clench, the collector, who has always had a special interest in the West Indies.

SPHAERODACTYLUS CLENCHI sp. nov.

Sphaerodactylus difficilis: Mertens, 1939: 43 (part); Cochran, 1941: 115 (part), including plate on page 116.

Holotype: MCZ 43706, a male, from Samana (= Santa Barbara de Samana), Samana, Dominican Republic, collected by William J. Clench, August 1937.

Paratypes: DOMINICAN REPUBLIC. All from *Samana.* With the same data as the type: MCZ 43707-9, 57151-65, USNM 107621-30; the same locality, Samana (Santa Barbara de Samana): AMNH 40630 and 19 untagged examples, William G. Hassler, October-December 1929, AMNH 40110, 90167, J. King, 1929; larger of three islands near Las Flechas: AMNH 41987, William G. Hassler, November 9, 1929; Rio San Juan: USNM 74942, Gerrit S. Miller, Jr., March 1927; "Samana and Laguna": USNM 65781, W. L. Abbott, March 1923; Sanchez: CM 8169, FMNH 5963 (4 specimens), Emil Kaempfer, March 1924; just Samana Province (no more exact locality): USNM 75001-2, Gerrit S. Miller, Jr., February 22, 1925, AMNH 49882, William G. Hassler, July 28, 1935; Samana, whether city or province unknown: MCZ 5451, M. A. Frazar, June 1882.

Diagnosis. Apparently most closely related to *S. caicosensis* Cochran from which it differs in having a longer snout, a larger number of lamellae under the 4th toe (overlap in one specimen of *caicosensis,* i.e. 12-14 [15] in 63 specimens of *clenchi* as compared with 9-11 [12] in *caicosensis);* it also differs in coloration: both sexes of *clenchi* are variously spotted and marked with darker and sometimes lighter, while female *caicosensis* is barred, and markings are wholly or mostly confined to the head in the male. The new form is less closely related to *S. notatus difficilis* but has been confused with that form, from which it differs in much smaller scales and in coloration.

Description. (Paratype variation in parentheses.) Snout of moderate length and acuteness; distance of eye from tip of snout greater than distance of eye to ear; rostral with median groove; nostril between supranasals separated by one scale (one specimen with them in contact, three with them separated by two scales); three large and one small supralabial to below center of eye; head above and on sides covered with small juxtaposed keeled scales, larger and mostly keeled on snout; scales on dorsum enlarged, elongate, keeled, and subimbricate; the more granular scales of the neck appear anterior to the forward level of the shoulder, the dorsals, however, decidedly smaller than those located more posteriorly at the point just mentioned (also in paratypes); scales in standard distance 14 (11-14, subadults sometimes going to 16); 52 dorsal scales between rear of hind limb and front of shoulder (45-60); 62 scales around body at midbody (53-68); 13 lamellae under the 4th toe (12-14 [15 in one specimen]); mental somewhat larger than rostral; two large infralabials followed by a small one to center of eye; two small, rather irregularly shaped scales behind the mental; behind these the scales decrease in size posteriorly to throat, increase in size on throat and chest and again on belly; smooth, except some very slight keeling on throat (also in some of the paratypes); tail in type regenerated, that of paratype MCZ 43707 apparently not, showing scales like those of dorsum, more imbricate and somewhat larger near base, not keeled near terminus; below, with scales like those of belly, but larger.

Coloration in alcohol. Above, light brown, heavily dotted, spotted, and vermiculated with dark brown including head, limbs and tail. Below, brownish white, underside of head and throat dotted with dark brown, elsewhere slightly washed or marked with the same color, especially at the sides of the belly.

In the paratypes, both above and below, often less heavily marked than the type, some of both sexes being virtually unmarked. Above, female and immature specimens tend to have the spots or dots on the neck and posterior part of the head arranged in longitudinal rows. Both sexes sometimes have whitish spotting on the body and one or more short longitudinal streaks of the same color starting at the posterior part of the eye and extending on to the neck.

Measurements (in mm). Type, MCZ 43706: length, head and body, 33; tail regenerated. Largest paratypes, duplicates with AMNH 40630 (2): head and body, 34; tail broken off and missing.

Remarks. At Sanchez, both the new form and *S. notatus difficilis* occur.

It was first thought that the two specimens (MCZ 44395-6) from Sanchez might be intermediate between *clenchi* and *difficilis;* the scale counts of both seemed rather high. The higher dorsal count from rear of hind limb to front of forelimb, at 43, was one higher than the highest for other *difficilis,* while the higher count around the body, at 54, was just equaled by other *difficilis.* The 10 for the standard distance of both these examples is one higher than the highest for the other *difficilis.* However, these two show typical *difficilis* coloration (male and female), and the examples of *clenchi* from Sanchez appear to be typical. There is, therefore, no real evidence of hybridization or intergradation. *S. caicosensis* appears to be the nearest relative of *clenchi* but presents enough differences to be regarded also as specifically distinct.

Since what is known as the Samana Peninsula is at best incompletely joined to the main island of Hispaniola even now, and formerly, even in historic times, was completely separated from it, there is an evident bar to the dispersal of *clenchi,* especially in more modern times. See Chapman Grant (1956:89).

Mertens (1939:43), under the heading of *Sphaerodactylus difficilis,* notes the smaller scales of Samana specimens as compared with the other specimens discussed. However, he did not believe he had sufficient material to name any of the populations discussed.

Identification aids. This form is characterized by its small scales, showing but little evidence of overlap in scale counts with other forms of the group. Most overlap is shown with some of the group with keeled throat scales.

Sphaerodactylus samanensis Cochran

Sphaerodactylus samanensis Cochran, 1932: 183, Boca del Infierno, Samana Bay, Dominican Republic.

Jay M. Savage (1954:328) regarded *samanensis* as a synonym of *S. n. difficilis.* However, what Savage regarded as *difficilis* has been here described as yet another race of *notatus (savagei).* No real scale differences between *difficilis* and *savagei* have been found, the differences being chiefly in coloration and in the shape of the male escutcheon. *S. samanensis,* on the other hand, differs from *savagei* in having the supranasals in contact, an extension rearward of the dorsal neck granules to the level of the insertion of the fore limb, and paired dorsal bands in the female (the only sex known). The scale counts for the three paratypes viewed are as

follows: in standard distance 8-9; dorsal scales from rear of hind limb to front of shoulder 36-38; scales around body at midbody 44-47; lamellae under 4th toe 12-13. The largest paratype had a head and body length of 28 mm, one more than Miss Cochran's measurement for the type.

Material examined: DOMINICAN REPUBLIC. *Seibo.* Boca del Infierno: USNM 74971-3 (paratypes).

Identification aids. This form can be distinguished from all others treated here by having its supranasals in contact (a rare variation in *S. n. difficilis*), an extension rearward of the dorsal neck granules to the level of the shoulder, and the regular paired bands in the female (the only sex known). The bands of *S. n. juanilloensis* suggest these but are not evenly formed.

Key to the SPHAERODACTYLUS NOTATUS *group in Hispaniola*

1. Ventral scales smooth 6
   Ventral scales smooth except for keeled scales on throat or on throat and chest 2
2. Scales around middle of body 40-47 3
   Scales around middle of body 50-61 4
3. Throat scales slightly keeled over a limited area; lamellae under 4th toe usually 9-10; no scapular spot; maximum head and body length 26 mm ..... *brevirostratus enriquilloensis*
   Throat scales well keeled over a considerable area; lamellae under 4th toe 11; large, black square scapular spot; maximum head and body length 31 mm (only known from one male) ..... *lazelli*
4. Scales around middle of body 50-56, only throat scales keeled 5
   Scales around middle of body 61; chest scales as well as throat scales keeled; a curved, white streak on back of head; two white spots on dorsum at level of shoulders (female color unknown) ..*armstrongi*[1]
5. Dorsal scale count from rear of hind limb to front of shoulder 35-41; lamellae under 4th toe 9-11; throat black, spotted or marked with white, intensity variable; maximum head and body length 24 mm ..... *noblei*
   Dorsal scale count from rear of hind limb to front of shoulder 39-43; lamellae under 4th toe 11-13; throat whitish, speckled with dark brown; maximum head and body length 29 mm .....*altavelensis*
6. Dorsal scale count from rear of hind limb to front of shoulder 25-45; scales around middle of body 37-54 7
   Dorsal scale count from rear of hind limb to front of shoulder 45-60; scales around middle of body 53-68 .....*clenchi*

[1] Not included in key are two specimens referred with doubt to *armstrongi*. See under species heading the account of their variation.

7. Dorsal coloration without paired bands (unpaired bands in immature of *savagei*), or if paired, separated by pale color; supranasals usually separated, dorsal neck granules not extending to level of front of fore limb 8

   Dorsal coloration with paired bands (male coloration unknown), supranasals in contact, dorsal neck granules extending to level of front of fore limb ..... *samanensis*

8. Usually well-defined, dark, longitudinal streaks on venter, curved heart-shaped streak on back of head (like top of heart with the possible apex toward the snout), pale color inside this marking, sometimes a second, less distinct streak, following first. In males these head markings may become entirely obsolete, reduced to a few specks; scapular spot quite persistent even in males ..... *b. brevirostratus*

   No longitudinal ventral streaks; if a curved streak on back of head, this not heart-shaped or enclosing a lighter area; scapular spot present or absent 9

9. Above virtually unmarked, vestige of scapular spot (male coloration only known); snout very short; maximum length of head and body 26 mm ..... *darlingtoni*

   Above variously spotted, marked and banded with darker; snout not very short; maximum lengths of head and body 29-33 mm 10

10. Above heavily spotted, banded or washed with darker, male sometimes unmarked, with light head spotted with dark; female also sometimes with curved band on back of head, sometimes melanistic without markings 11

    Three longitudinal dark streaks on dorsal aspect of head and neck in female. Body of male usually rather obscurely speckled with darker, and head unmarked. Sometimes head lighter, marked with darker or speckles both on head and body ..... *notatus difficilis*

11. Scales, rear of hind limb to front of fore limb 36-44; scales around body at midbody 48-54 ..... *notatus randi*

    Scales, rear of hind limb to front of fore limb 25-34; scales around body at midbody 36-48 12

12. Scales around body at midbody 36-44; heavily spotted above including head. Females with some development of obscure head stripes. Immatures with bars on back ..... *notatus savagei*

    Scales around body at midbody 40-48; females often showing paired crossbars separated by lighter on back, two head stripes joining on rear of head. Males spotted above, showing tendency for spots to form into crossbars ..... *notatus juanilloensis*

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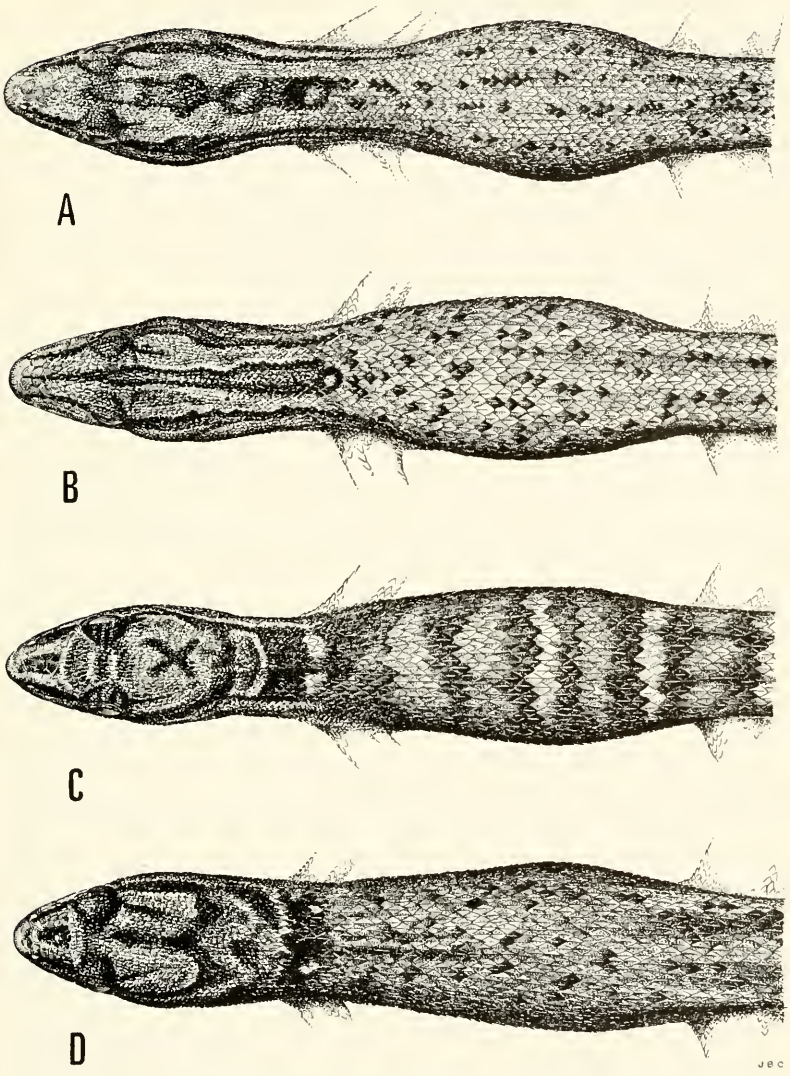
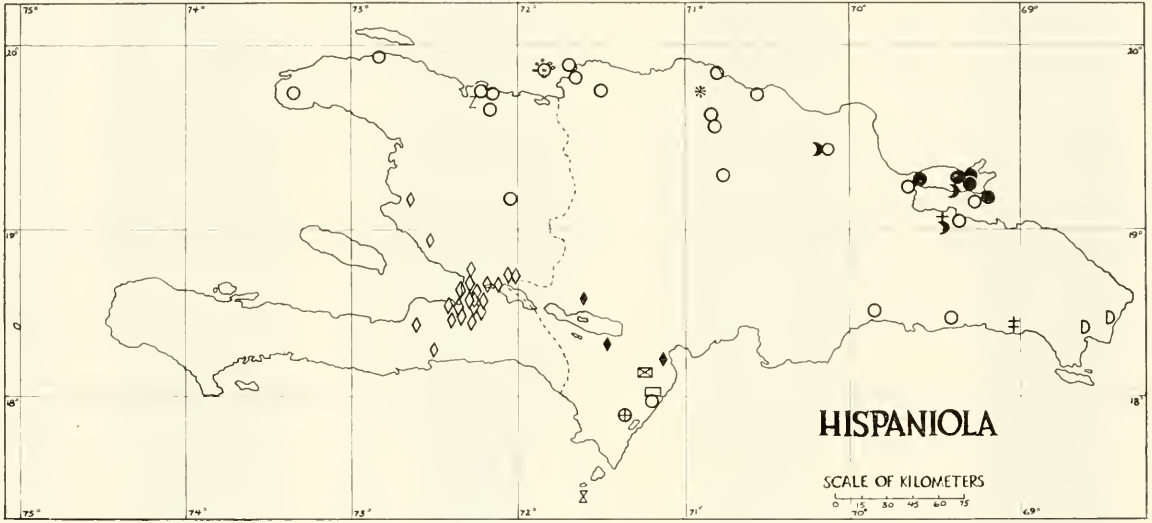


Fig. 1. A, *Sphaerodactylus notatus difficilis*, MCZ 78733, Licey Almedio, Prov. Santiago, Dominican Republic. B, *S. notatus notatus*, MCZ 31638, Key West, Florida. C, *S. notatus juanilloensis* holotype, MCZ 73901, Juanillo, Prov. Altagracia, Dominican Republic. D, *S. brevirostratus brevirostratus* holotype. MCZ 63234, 5 km S of Dufort, S of Leogane, Dept. de l'Ouest, Haiti.



○ notatus difficilis
D " juanillaensis
‡ " savagei
⊕ " randi
● clenchi
+ samanensis
◊ b. brevirostratus
♦ b. enriquilloensis
□ armstrongi
⊠ armstrongi?
Z lazelli
◗ noblei
✳ darlingtoni
⧖ altavelensis

Fig. 2. Distribution of forms of the *Sphaerodactylus difficilis* group in Hispaniola.

BREVIORA

Museum of Comparative Zoology

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ADDITIONAL NOTES ON BATOID FISHES FROM THE WESTERN ATLANTIC[1]

Henry B. Bigelow and William C. Schroeder

	Page
Introduction	2
Order Batoidei	2
Suborder Torpedinoidea	2
Family Torpedinidae	2
Torpedo nobiliana	2
Diplobatis pictus	3
Suborder Rajoidea	4
Family Rajidae	4
Raja bullisi	4
Raja cervigoni	5
Raja clarkii	8
Raja floridana	9
Raja fuliginea	11
Raja lentiginosa	13
Raja olseni	14
Raja teevani	14
Breviraja plutonia	15
Breviraja sinusmexicanus	15
Breviraja spinosa	16
Cruriraja rugosa	17
Family Pseudorajidae	18
Pseudoraja atlantica	18
Family Anacanthobatidae	18
Anacanthobatis americanus	18
Anacanthobatis longirostris	19
Springeria folirostris	20
References cited	22

[1]Contribution No. 1875 from the Woods Hole Oceanographic Institution.

INTRODUCTION

During the last fifteen years we have received for study a large number of interesting batoids, together with some cyclostomes, sharks, and chimaerids, trawled by U.S. Fish and Wildlife vessels, chiefly the "Oregon" and the "Silver Bay" but also the "Combat," "Pelican," and "George M. Bowers." Most of these were taken in the Gulf of Mexico, the Caribbean, and along the coast of South America as far south as 01°49′N off the mouth of the Amazon, with a few from along our eastern coast to the southward of Cape Hatteras. Bottom trawling depths ranged from 40 to 750 fathoms (65-1370 m), chiefly between 100-500 fathoms (183-915 m). Many new species are included in our various reports from 1951 to 1965, listed in the references cited.

The present account includes eighteen species of batoids, none of them new, but they yield additional information as to range, depths of capture, size, etc. They were taken at 95 "Oregon" and 10 "Silver Bay" stations which fall within the following depth ranges: 10 at 40-100; 11 at 101-200; 60 at 201-300; 13 at 301-400; 8 at 401-500; and 3 stations at 501-600 fathoms, ranging from northern Florida to Venezuela, including the Gulf of Mexico. Also included is a summary of previously published capture records for each species.

We thank the various investigators who collected and preserved these specimens, and Harvey R. Bullis, Jr., of the U. S. Fish and Wildlife Service for placing them at our disposal.

Order BATOIDEI
Suborder TORPEDINOIDEA
Family TORPEDINIDAE
Torpedo nobiliana Bonaparte 1835

Our recent accounts (1962, 1965) of this species include the capture of 12 specimens, ranging in length from 211 to 700 mm, trawled in various localities ranging from North Carolina to the Caribbean coast of Panama (9°00′N, 81°23′W), including the Gulf of Mexico, in depths of 10 to 290 fathoms (18 to 530 m). It is known in the western Atlantic from as far north as the offing of southern Nova Scotia and in the eastern Atlantic from northern Scotland to the Mediterranean, Azores, Madeira, and tropical West Africa.

The present collection includes 12 specimens, 205 to 393 mm long, 3 from the east coast of Florida, 1 from the east coast of Hispaniola, and 8 from off the coast of Venezuela, in 40 to 240 fathoms (73 to 440 m), "Oregon" stations 4393, 4394, 4401, 4402, 4418, 5037, 5101, 5109 and "Silver Bay" stations 5188, 5530.

An examination of a number of recently obtained specimens, necessitates a modification of two descriptive characters given in *Fishes of the Western North Atlantic, Part 2* (Bigelow and Schroeder, 1953, p. 94), stated as "disc appreciably shorter (less than 80 per cent) than its breadth" and "height of caudal fin not greater than distance from its own upper origin to origin of first dorsal."

Four males 215-900 mm long and seven females of 211-613 mm have a disc length ranging from 77 to 90 per cent of the disc width, only two individuals falling below 80 per cent. The height of the caudal is greater, 1.10 to 1.38 times, than the distance from the upper origin of the caudal to the origin of the first dorsal on 10 specimens and less, 0.95 times, on only one.

In color, this ray has been described as dark chocolate to purplish brown above, either uniform or with a few obscure darker spots, and white below, but with the edges of the disc and pelvics of the same hue as the upper surface, the tail with irregular dark markings. Our specimens likewise are so colored above but the markings below on several are grayish. It is reputed to reach a weight of about 200 pounds.

Diplobatis pictus Palmer 1950

The type of this species was taken off Georgetown, British Guiana, a female 137 mm in total length. Our recent account (1962) includes 24 specimens, 77-164 mm long, from the mouth of the Amazon 02°29′N to British Guiana 09°31′N in 9-50 fathoms (16-92 m).

The present collection includes 3 males of 85-159 mm and 3 females of 140-196 mm from 12°19′-12°37′N, 70°34′-71°10′W, off the mouth of the Gulf of Venezuela, in 40-65 fathoms (73-119 m), "Oregon" stations 4393, 4394, 4401, 4402.

In our 1962 account we mentioned certain characters that supposedly differentiated *D. pictus* from *D. guamachensis* Martin 1957. Thus we stated that in 21 specimens of *pictus*, 77 to 164 mm long, the width of disc ranges from 38.8 to 50.0 per cent, the length

of disc from 38.8 to 48.0 per cent, and the breadth of pelvics from 28.7 to 36.6 per cent of total length; also that the lateral folds originated between the rear end of the first dorsal base and the origin of the second dorsal. In a personal communication received from Dr. Martin in 1959, based on 4 specimens of *guamachensis* 56.5-70.9 mm long (including the type), from the Gulf of Cariaco, Venezuela, the above proportions are given as 53.0 to 58.1, 50.3 to 54.5, and (on two specimens) 23.8-26.0, respectively, the lateral folds originating "immediately behind the origin of first dorsal."

The color and markings on *pictus* vary considerably and our earlier collection does not include any with the design of *guamachensis* with its irregular dark bars and spots. However, in our present collection of 6 specimens, two males 85 and 196 mm long, respectively, are marked much like Martin's illustration, though somewhat more elaborately. This variation in the markings on *pictus* recalls that of *Narcine brasiliensis*. Furthermore, they fall in line with the proportional dimensions of all our other *pictus* and also confirm that the lateral folds originate between the dorsal fins and not immediately behind the origin of the first dorsal. We therefore consider *D. guamachensis* a synonym of *D. pictus*.

The known range of this species now extends from the offing of the Gulf of Venezuela to that of the Amazon River and in depth from 9 to 65 fathoms (16-119 m).

Suborder RAJOIDEA

Family RAJIDAE

Raja bullisi Bigelow and Schroeder 1962

Specimens previously recorded (1962, 1965), 166 to 478 mm long, range from Dry Tortugas, Florida, 24°36′N, to the coast of Surinam, 07°15′N, in 110-300 fathoms (201-549 m).

Three specimens are included in the present collection: a 205 mm female from off Santa Marta, Colombia, 11°08′N, 74°23.8′W, in 100 fathoms (183 m), "Oregon" station 4856; a 280 mm female 11°31′N, 60°51′W, in 240-250 fathoms (440-457 m), station 5029; and a 370 mm male 11°36.5′N, 62°46.5′W, in 200-240 fathoms (366-440 m), station 5037, from the offing of the Gulf of Paria, Venezuela.

Bullisi closely resembles *Raja teevani* but its persistent nuchal thorn, somewhat broader tip of snout, and somewhat greater space between the dorsals (0.23 to 0.45 times the first dorsal base)

distinguish it from the latter which lacks a nuchal thorn, has a very sharp tip of snout, and dorsals that are confluent or with an interspace seldom exceeding 0.15 times the first dorsal base.

RAJA CERVIGONI Bigelow and Schroeder 1964

Previous records of this species include: an immature male of 357 mm, the holotype, from 10 miles (16 km) northeast of Carúpano, in 20-30 fathoms (37-55 m), Museo Historia Natural La Salle, Venezuela, No. 873; a male of 206 mm, and a female of 229 mm from Punta Araya, Estado Sucre, in about 20 fathoms (37 m), off the eastern part of Venezuela; and a male of 235 mm from off the Guianas, 07°25′N, 54°35′W, in 75-80 fathoms (137-146 m), "Oregon" station 2289.

The present collection includes 2 males, 144 and 506 mm long, respectively, the latter mature, and a female of 418 mm, from off the Peninsula de Guajira, Venezuela, 12°29′N, 71°54′W, in 95 fathoms (174 m), "Oregon" station 5685.

Description of mature male. Proportional dimensions in per cent of total length.

Disc. Extreme breadth 69.5; length 50.2.

Snout length. In front of orbits 10.7; in front of mouth 13.5.

Orbits. Horizontal diameter 4.4; distance between 4.2.

Spiracles. Length 2.8; distance between 6.1.

Mouth. Breadth 8.1.

Exposed nostrils. Distance between inner ends 7.9.

Gill openings. Length 1st 1.7; 3rd 1.7; 5th 1.5; distance between inner ends, 1st 13.8; 5th 7.3.

First dorsal fin. Height 2.8; length of base 4.9.

Second dorsal fin. Height 2.8 length of base 4.9.

Pelvics. Anterior margin 12.1.

Distance. From tip of snout to center of cloaca 46.5; from center of cloaca to 1st dorsal 36.5; to tip of tail 53.5; from rear end of 2nd dorsal to tip of tail 3.4.

Interspace. 1st and 2nd dorsals 3.8.

Disc 1.38 times as broad as long; maximum angle in front of spiracles 99°; anterior rays of pectorals extending 50 per cent of distance from level of orbits toward tip of snout, the latter projecting; rostral process firm, extending to tip of snout; anterior margins of disc slightly convex in front of spiracles, thence concave and straight toward outer corners which are sharply rounded, the width of disc across anterior edge of orbits 25 per cent of total length of specimen; posterior margins and corners and inner

margins all rounded. Axis of greatest breadth 71 per cent of distance back from tip of snout to axils of pectorals. Tail rather slender, the lateral folds low down, narrow, originating a little in advance of tips of pelvics, reaching tip of tail; length of tail from center of cloaca to origin of first dorsal 0.78 times as great, and to its tip 1.15 times as great as distance from center of cloaca to tip of snout.

A row of 9 thorns along anterior and inner margins of one orbit, 10 along the other, and 3 minute thorns opposite inner margin of each spiracle with several small ones over tip of rostrum. Three prominent thorns along midline in the nuchal region, followed by a space and the next thorn, a tiny one, opposite the axils of pectorals, with 6 more to opposite tip of anterior pelvic lobe, then 22 thorns alternating large and small in an unbroken series to the first dorsal fin; 2 thorns in front of second dorsal. A row of 21 thorns low down each side of the midrow on tail, more or less alternating in size, beginning a little in advance of tips of posterior pelvic lobe and reaching to opposite origin of first dorsal. Malar thorns prominent, sharp, backward pointing, each patch consisting of 3 to 4 rows 40 mm long and 16 mm wide. Alar thorns well developed, each patch about 60 mm long and 13 mm at widest, the rows irregular, as many as 5 rows anteriorly reducing to a single thorn posteriorly. A band of fine prickles along edge of disc from opposite posterior malars to outer angle. Upper surface otherwise smooth. Lower surface with a patch of prickles on end of snout merging with a narrow band of prickles along edge of disc extending to about opposite mouth; otherwise smooth below.

The claspers are massive, extending 75 mm beyond the tips of pelvics.

Color. Upper surface plain medium brown. A prominent ocellus on each side of disc, situated a little posterior to the greatest axis of disc, its center from the midline of disc a distance about equal to that from tip of snout to center of orbit; distance between centers of ocelli 133 mm, and between centers of ocelli and centers of orbits 127 mm. The ocelli have a pale center surrounded by a roundish area of solid dark brown the diameter of which is about 9 to 11 mm, thence a pale area surrounded by a narrow, somewhat broken dark brown circle about 21 mm in diameter and finally with an outside narrow pale circle. Lower surface of disc and pelvics margined with a band of pale grayish, the tail with brownish blotches.

The 144 mm male has a disc 1.45 times as broad as long; maximum angle in front of spiracles 109°; contour of disc about the same as the 506 mm male, except that width across anterior edge of orbits is 34.7 per cent of total length of specimen; axis of greatest breadth 72.6 per cent; length of tail to origin of first dorsal 0.72 times as great and to its tip 1.08 times as great as distance from center of cloaca to tip of snout. Two thorns along anterior margin and 1 at inner posterior margin of each orbit; 1 nuchal thorn; a row of 16 large, sharp, thorns in midline, evenly spaced, from opposite axils of pectorals to first dorsal and 2 between dorsals; a row low down each side of midrow, from opposite tip of pelvics to interdorsal space, 11 on one side 12 on the other, in size about the same as those in midrow; otherwise smooth above. Smooth below except for a single row of 6 to 7 very small spines along edge of disc between tip of snout and nostrils. Claspers not reaching tip of pelvics. The distance of the center of each ocellus from the midline of disc is equal to that from tip of snout to anterior margin of orbit; distance between centers of ocelli 40 mm and between centers of ocelli and centers of orbits 35.5 mm. The ocelli have a dark brown center and an outside solid dark brown circle 6 mm in diameter, with a pale area between and another surrounding the colored areas. The lower surface is marked with a broad outer band of gray from opposite mouth to axils of pectorals, its inner margin irregular, and with a pair of irregular grayish blotches at the origin of the anterior pelvic lobes and on the tips of the posterior lobes, the tail with two vague grayish areas posteriorly.

The 418 mm female agrees closely with the small male in proportional dimensions. The ocular and nuchal thorns are of the same number as on the 506 mm male but the midline thorns are more numerous, there being 6 very small ones from opposite the ocelli to the axils of pectorals followed by 30, alternating large and small, to the first dorsal, with 2 small thorns and 1 large between the dorsals. The side row contains about 35 thorns extending from near axils of pectorals to opposite the second dorsal, more or less alternating in size, but the posterior 5 or 6 very small. The prickles along the edge of disc anteriorly, above and below, are similar to those of the large male. The distance between the centers of the ocelli is 117 mm and between centers of ocelli and centers of orbits 98 mm. Color above and below similar to the large male. The tooth count on the 7 specimens thus far examined ranges from $\frac{34}{32}$ to $\frac{42}{40}$.

RAJA CLARKII Bigelow and Schroeder 1958

Our previous records of *R. clarkii* (1958, 1962, 1965) include a total of 4 males 228-665 mm long, and 4 females of 176-747 mm. Four were trawled in the northern part of the Gulf of Mexico, 3 off the coast of Nicaragua and 1 off Panama, in depths ranging from 200 to 300 fathoms (366-549 m).

The present collection includes 3 males of 330-710 mm from the north central part of the Gulf of Mexico, "Oregon" stations 4701, 4703, 4716; 6 males of 265-525 mm and 2 females of 256-370 mm from off Colombia, stations 4841, 4882, 5689, 5690, 5722; and a male of 351 mm and 2 females of 250-275 mm off Venezuela, stations 4438, 4456. These stations range in depth from 220 to 500 fathoms (400-915 m).

This species is characterized among western Atlantic rajids by the presence of a band of formidable and very sharp thorns extending along the margin of the lower surface from the tip of the snout almost to the outer corners of the disc. An amplification of previous descriptions follows.

The median row of thorns, which is continuous from the nuchal region to the first dorsal fin, number from 30 to 43 of which 4 or 5 are in the nuchal-scapular area followed by about 7 to opposite axils of the pectorals. The total number of thorns does not necessarily increase with the size or age of the skate, for a male and a female, 256 and 324 mm long, respectively, have 43 thorns while a male and a female of 710 and 747 mm have only 37-38 in the median row. There is a triangular patch of thorns in the nuchal-scapular area which may have but 1 thorn on each side of the mid-row or as many as 4 or 5. In arrangement, the orbital thorns on most of our specimens, including the largest, consist of 2 anterior, 1 posterior, and from 1 to 3 aside the spiracles.

The color of the upper surface of all the specimens we have seen is brown with darker punctulations scattered over the disc, pelvics, and more or less on the tail. Some have conspicuous white spots while others lack them. Thus 5 specimens, 250-747 mm long, have 3 pairs of spots, 8 of 265-580 mm have 1 pair, and 8 of 176-525 mm lack them. One specimen of 710 mm has 1 pair anteriorly and 1 spot on one side posteriorly. It is noteworthy that the spots are located in the same parts of the disc. Thus the anterior pair is opposite the spiracles, the median pair, slightly closer together, opposite the scapular region, and the posterior pair a little in advance of axils of pectorals and about in line with the anterior pair. Where but one pair is present it is located anteriorly. In shape the

spots may be barlike, oval, or spherical, and in size, if roundish, from less than to about equal to the area of the orbit, or, if barlike, about as long or longer than the diameter of the orbit. The lower surface is white with a broad grayish band, its inner margin irregular (Bigelow and Schroeder, 1958, fig. 9; 1965, fig. 1) extending on most specimens from a little in advance of the outer angles of disc to the axils of the pectorals and along the rear margin of the pelvics, but on several this band originates near the tip of the snout. Also, a few small gray spots or blotches may be present here and there on the disc, including one each side of the cloaca.

The largest male, 710 mm in length, is approaching maturity as the claspers are well developed, extending 56 mm beyond the tips of the pelvics, and a few of the alar thorns are exposed.

The present known range of this species is from the northern part of the Gulf of Mexico to the offing of Colombia (12°30′N, 72°08′W) in 200-500 fathoms (366-915 m).

Raja floridana Bigelow and Schroeder 1962

The original account of this species includes 27 specimens 158-448 mm long, and 1, the holotype of 772 mm, trawled between Cape Lookout, North Carolina, and Dry Tortugas, Florida, 34°21′ to 24°17′N, in 170-225 fathoms (311-412 m).

The present collection includes 32 specimens, 145-585 mm long, males and females about equally divided, taken at 12 "Oregon" stations (5097, 5098, 5100, 5101, 5102, 5106, 5107, 5113, 5119, 5234, 5295, 5482) and "Silver Bay" station 5454. These fall within a small area between the offings of Cape Kennedy and St. Augustine, Florida, 28°00′-29°58′N, 79°51′-80°10′W, in 160-213 fathoms (293-390 m).

In general appearance *floridana* resembles *R. laevis* Mitchill, 1815, but it differs from *laevis* in a proportionately longer snout, wider disc, usually a shorter tail, and smaller dorsal fins. Thus, on 6 males and 3 females of *floridana* 298-772 mm in total length, the distance from the tip of snout to the mouth is 19.5-24.9 per cent, the width of the disc 73.2-81.2 per cent, the length of the tail from center of cloaca 43.8-47.1 per cent, and the distance from origin of first dorsal fin to the rear end of base of second dorsal 8.4-12.1 per cent of total length. These proportions on 2 males and 1 female of *laevis,* 506-542 mm long, are 17.0-18.0 per cent, 68.0-71.0 per cent, 49.7-51.7 per cent and 14.5-14.8 per cent, respectively. On 7 *floridana* 158-240 mm long the distance from snout to mouth is 18.0-21.1, length of tail 46.2-50.5 and there are 8 to 10 tail

thorns, whereas on 5 *laevis* of 177-195 mm these proportions are 14.1-17.8 and 54.2-58.7 and the tail thorns 13 to 18.

We are indebted to George C. Miller of the U. S. Fish and Wildlife Service for pertinent data on a collection of 17 specimens, 155-252 mm long, and 1 of 465 mm, all taken between the offing of South Carolina and the Straits of Florida in 180-220 fathoms (329-402 m), except one from 29°04′N, 88°31′W, "Oregon" station 3724, the latter extending the range to the northern part of the Gulf of Mexico. Four of these specimens have tail lengths of 50.9-53.8 per cent of total length, a little greater than our 50.5. The tail thorns number 8 to 12 except on the one of 465 mm which has 15. Three have 2 anterior orbital thorns and 1 posterior, the others 1 anterior and 1 posterior.

The armature of the upper surface, at least on sizes up to 585 mm, is limited to the orbital thorns, a single midrow of rather inconspicuous thorns from somewhat in advance of the axils of pectorals to the first dorsal fin, and to 1 or 2 or no thorns between the dorsals. But there is not necessarily a progressive increase in the number of thorns with the size of the skate. Up to a length of about 400 mm most of our specimens have 1 anterior and 1 posterior orbital thorn, but a few, including the smallest, have 2 anterior and 1 posterior. One of 585 mm has 10 or 11, and in addition 2 aside each spiracle, while another of 488 mm has only 5 or 6 thorns along the margin of each orbit with 1 aside each spiracle.

The thorns in the midrow usually number from 8 to 14 on specimens up to a length of about 400 mm, but two of 432-435 mm have only 3 (there is evidence that some thorns were shed and others still embedded), while one of 585 mm has 23, the anterior 13 being smaller than the posterior 10. The lower surface is smooth.

The immature 772 mm holotype has 12 small thorns along the anterior and inner margins of each orbit with 3 very small ones in advance of these while the midrow contains 25 small thorns of assorted sizes, with a few rather large ones. The lower surface is densely prickly in advance of axis through the mouth, except for a nearly smooth area immediately in front of mouth. A band of prickles extends along the margin of the disc from the snout to about opposite the 4th or 5th gill openings, the remaining lower surface, including the tail, being virtually smooth.

The maximum angle of the disc in front of spiracles ranges from 81° to 94°, except 74° on the holotype. The teeth range in number

from 27 to 38 in each jaw, and have a low triangular cusp, even on the smallest specimens of both sexes. In color, the smallest specimens are light brown above, with vague dark brown irregular spots about half as large to as large as the orbit, and the tail has 5 dark bars about equally spaced. The lower surface is whitish with a narrow dusky margin on the outer angles of disc. Our larger specimens lack the spots, and below are usually plain grayish white, some of them partly brownish. All, small to large, have dark-ringed mucous pores on the under surface, most numerous anterior to the axis through the mouth and immediately below the lower jaw.

It is of interest that all of the many specimens so far collected have been taken within the rather limited depth range of 160-225 fathoms (293-412 m), although many trawl hauls, both shoaler and deeper, have been made within the known latitudinal range of this species.

Raja fuliginea Bigelow and Schroeder 1954

Until recently this species had been known only from the holotype, a juvenile male 306 mm long, USNM No. 163367, taken at "Oregon" station 534, in the northwestern part of the Gulf of Mexico, 27°32′N, 93°02′W, in 400-450 fathoms (732-823 m). A second specimen, a female of 330 mm, was trawled at "Oregon" station 4147, about 45 miles southwest of Dry Tortugas, Florida, 24°12′N, 83°32′W, in 500 fathoms (915 m) (Bigelow and Schroeder, 1965).

We now have 14 more specimens, as follows: 9 from the western and northern parts of the Gulf of Mexico, "Oregon" stations 4701, 4711, 4713, 4802; 2 off Isla del Rosario, Colombia, station 4883; 1 from about 40 miles northwest of Caracas, Venezuela, station 4449, and 2 off Curaçao, station 4416, males and females evenly divided, total lengths 224-445 mm. The range in latitude is from 27°42′ to 10°15.5′N, in longitude from 96°00′ to 67°38′W. All were taken in 500-600 fathoms (915-1098 m).

In our original account (1954), *fuliginea* was compared with *R. bathyphila* Holt and Byrne 1908 which it most closely resembles in general arrangement of thorns and prickles, in proportional dimensions and in the very dark coloration of the lower surface of disc and tail. But *fuliginea* differs from *bathyphila* in a more obtuse anterior contour and especially in the fact that the entire lower surface of the tail, apart from a very narrow median stripe, is densely prickled from base to tip, whereas it is naked in *bathyphila*.

Also, the prickles on the upper surface of disc and tail are coarser than on *bathyphila* and there are no naked areas.

Proportional dimensions in per cent of total length of all 14 specimens:

Disc. Extreme breadth 43.7-51.8; breadth across anterior margin of orbits 24.6-28.6; length 37.5-49.0.

Snout length. In front of orbits 9.1-10.3; in front of mouth 10.0-13.2.

Orbits. Horizontal diameter 3.4-4.6; distance between 2.7-3.6.

Spiracles. Length 2.1-2.9; distance between 5.7-7.3.

Mouth. Breadth 5.3-7.8.

Exposed nostrils. Distance between inner ends 6.2-7.3.

Gill openings. Length, 1st 1.4-1.8; 3rd 1.4-1.8; 5th 1.1-1.5; distance between inner ends, 1st 10.7-14.8; 5th 5.8-8.5.

First dorsal fin. Height 2.5-3.6; length of base 4.6-6.1.

Second dorsal fin. Height 2.5-3.5; length of base 4.5-6.3.

Pelvics. Anterior margin 10.1-13.4; origin to tip 13.4-17.5.

Distance. From tip of snout to center of cloaca 35.2-44.0; from center of cloaca to 1st dorsal 42.4-48.8; to tip of tail 56.0-64.8; from rear end of 2nd dorsal to tip of tail 2.7-4.5. Interspace: 1st and 2nd dorsals 0.0.

In armature, the upper surface of the disc, tail, and posterior lobe of pelvics, is densely covered with small sharp prickles. The dorsals, caudal fin, and the skin over eyes also are prickly. The orbital thorns, in various combinations, range from 2 at the inner margin of each orbit to 5 or 6 at the anterior and inner margins. There may be, in addition, a thorn aside one or both spiracles, or this thorn may be lacking at both. All these thorns are usually rather prominent but are very small on several specimens. The thorns on the nuchal-scapular region are in most cases arranged in a triangular patch, with 2 to 4 in the midrow and 1 or 2 on each side of these, the exceptions being 3 on each side, or none, only 1 thorn in the midrow and, on a male of 445 mm, all the nuchal-scapular thorns are lacking. The thorns in the midrow, including the nuchal region, number from 15 to 29, the fewest (15 and 19) being on the larger specimens, a male of 445 mm and a female of 412 mm in total length, and the most (28 and 29) on a male of 224 mm and a female of 293 mm. They may continue from the scapular region with no interruption, or after a short space, or resume as far rearward as opposite the axils of the pelvics, and extend to the dorsal fin or fall short of the dorsal a distance as much as that between the spiracles. In addition to the midrow there is

a siderow of thorns, usually irregular, beginning opposite the axils of the pectorals or as far rearward as about the tips of the pelvics and ending, when complete or nearly so, about opposite the origin of the first dorsal. But on some specimens the row runs out well in advance of the dorsal, and on one, a male of 428 mm, the row is virtually nonexistent, there being only 2 or 3 thorns on each side of the midrow. The thorns in the side row may be of the same size as those in the midrow, or somewhat larger or smaller.

The lower surface of disc and pelvics is smooth but the tail is densely set with prickles or thornlets, similar to those of the upper surface, but on some specimens these are lacking or sparse along a very narrow median stripe.

The color of the disc and pelvics is plain grayish above, ranging from light to rather dark. The tail may be of the same hue or somewhat paler. Below, the disc and pelvics are dark gray (3 specimens), dark brown (7 specimens), or blackish brown (4 specimens) some with pale areas around the entrance to cloaca and/or on end of snout, around the jaws, and at tips of pelvics. The tail is of the same shade, or slightly darker than it is above.

Raja lentiginosa Bigelow and Schroeder 1951

Many specimens of this skate, 80 to 435 mm in total length, have been trawled by the "Oregon" in the Gulf of Mexico, where it is widespread, southward to the offing of Nicaragua (11°27′N, 83°11′W) within depths of 29-305 fathoms (53-558 m). The present collection includes 6 more of 226-418 mm, from the northern Gulf taken in 100-240 fathoms (183-439 m), "Oregon" stations 4614, 4616, 4696, 4705.

There is a band of thorns along the median zone of back and tail, in 3 rows anteriorly, thence merging to 5 rows, and again in 3 rows as the tail narrows. These thorns have been described as originating in the nuchal region but we have since seen many specimens on which the band begins posterior to the nuchal region as much as the distance from tip of snout to rear margin of orbits. In some instances the median row originates slightly in advance of the side rows, but usually it begins posterior to them.

The upper surface everywhere is densely freckled with light to dark brownish and whitish spots, including the tail, pelvics and claspers, distinguishing *lentiginosa* from *R. garmani* (Whitley, 1939) which it closely resembles, the latter having fewer spots which are grouped mostly in a distinct rosette pattern.

The lower surface is white, variously marked with grayish which may be in the form of a group of blotches, mostly fused, on each pectoral, or a broad band with an irregular inner margin extending from opposite the first pair of gill openings to as far as the inner margin of the pectorals. Some have an elongate blotch on the claspers and a blotch on the anterior and/or posterior pelvic lobes. Tail white.

In the original account of *lentiginosa* the second dorsal and the caudal fin are shown as confluent, but we have found a few specimens with a short space between these fins.

Raja olseni Bigelow and Schroeder 1951

Previous accounts (1951b, 1953, 1962) of this species include 15 specimens, 151-568 mm long, trawled in 53-130 fathoms (97-238 m) at 9 stations by the "Oregon" and at 1 by the "Silver Bay." All were taken in the northern and northwestern part of the Gulf of Mexico. The present collection includes two males of 161-196 mm, and a female of 335 mm, from "Oregon" station 4695, 26°16′N, 90°13′W, in 50-53 fathoms (92-97 m), in the same region as above. We include this record to emphasize how restricted is the present known range of this species in spite of the many bottom trawl hauls made by the "Oregon" and other vessels in other parts of the Gulf and along the outer coast between North Carolina and the offing of the Amazon.

Raja teevani Bigelow and Schroeder 1951

Accounts of this species (1951b; 1965) include 6 males and 11 females, 175-635 mm long, of which 4 were trawled off Pensacola, Florida (3 "Oregon" stations), 1 at the northwest edge of Great Bahama Bank, and 1 in Santaren Channel ("Silver Bay" stations), and 11 off the coasts of Honduras and Nicaragua, the latter between 16°43′ and 12°25′N (9 "Oregon" stations), in depths of 240 to 400 fathoms (439-732 m). We now have 5 more, all males, 306-840 mm long, of which 4 were taken in the northwestern Gulf of Mexico ("Oregon" stations 4703, 4709, 4729, 4800) in 300-400 fathoms (549-732 m) and 1 of 500 mm from off Riohacha, Colombia, at 11°50′N, 73°05′W (station 4911), in 175-190 fathoms (320-348 m).

Teevani closely resembles *R. floridana* from which it differs in having fewer orbital thorns when about half grown and larger. Thus, on sizes up to about 600 mm there are, with few exceptions,

1 or 2 anterior thorns and 1 posterior, and on the largest, of 840 mm, only 5 thorns along the margin of one orbit and 3 at the other. Whereas young *floridana* up to about 300 mm have 1 anterior and 1 posterior thorn; at 450 mm there may be as many as 8 or 9 at each orbit and on one of 772 mm, the largest seen, there are 12 along the anterior and inner margins and 3 more in advance of these.

Minute prickles are present on the upper surface of the disc on *teevani* of all sizes, on some anteriorly only, but on others scattered all over the disc. They are lacking on our *floridana,* except for the large one of 772 mm on which the end of the snout is densely covered with coarse prickles and small thorns blending into minute prickles to about opposite the spiracles, the rest of disc smooth. On the lower surface of *teevani* prickles are present anterior to the mouth and in a band along the edge of disc from near the end of snout to about opposite the first pair of gill openings, on small individuals as well as large, but *floridana* is perfectly smooth below, up to a length of at least 450 mm, though prickles are present anteriorly on the 772 mm specimen.

Teevani and *floridana* were in no case taken at the same station. The known range of the latter is from the offing of Cape Lookout, North Carolina to Dry Tortugas, Florida, in 160-225 fathoms (293-412 m).

Breviraja plutonia (Garman) 1881

Many specimens of this species have been recorded (Bigelow and Schroeder, 1953, 1962) from the offing of Cape Lookout, North Carolina, and southward to an area centering about 30 miles southwest of Dry Tortugas, Florida, in depths of 160-400 fathoms (293-732 m), in size from 62 to 270 mm. The present collection includes 100 specimens 76-257 mm long, trawled between St. Augustine and Vero Beach, Florida, in 188-215 fathoms (344-393 m), "Oregon" stations 5075, 5077, 5089, 5097, 5115, 5231, 5233, 5483, 5484, and 7 specimens west to southwest of Dry Tortugas in 190-310 fathoms (348-567 m), stations 4335, 4356, 4558. One of the latter, 275 mm, is the largest we have seen.

Breviraja sinusmexicanus Bigelow and Schroeder 1950

All the previous captures of this skate have been recorded (1950, 1953, 1962, 1965) from the northern part of the Gulf of Mexico, except for one station in the Gulf of Campeche. There are 26

specimens in the present collection, also from this region and from the western part of the Gulf off the Mexican coast. These were trawled at "Oregon" stations 3681, 4580, 4581, 4583, 4606, 4614, 4616, 4697, 4703, 4709, 4729, 4730, 4776, 4800, 4808, 4809, 4816. The range in length, including specimens taken on all cruises, is from 78 to 360 mm, and in depth of capture from 170 to 500 fathoms (311 to 915 m), except for one station at 100 fathoms (183 m).

Breviraja spinosa Bigelow and Schroeder 1950

Previous accounts of this species include several specimens taken by the "Albatross" during the years 1885-1886 off Delaware Bay and North Carolina, stations 2624 and 2730, in 258 and 727 fathoms (472-1330 m), respectively. These were in very poor condition, their identity as *spinosa* was doubtful, and they cannot now be found for re-examination.

Published reports (1950, 1953, 1962) record a large series of *spinosa* ranging from the offings of Charleston, South Carolina (32°58′N), to the Guianas (07°05′N), in length 77-424 mm, trawled in 150-400 fathoms (274-732 m). Eighteen more have been taken at 7 "Oregon" stations (4428, 4854, 4912, 5039, 5689, 5690, 5722), from off Colombia, from south of Curaçao, and southwest of Grenada, 115-528 mm long, from depths of 257-400 fathoms (470-732 m). Following is a description of a mature male of 528 mm, much larger than any male previously seen (332 mm).

Proportional dimensions in per cent of total length.

Disc. Extreme breadth 58.5; length 46.2.

Snout length. In front of orbits 8.7; in front of mouth 10.4.

Orbits. Horizontal diameter 4.6; distance between 3.5.

Spiracles. Length 4.1; distance between 6.1.

Mouth. Breadth 7.4.

Exposed nostrils. Distance between inner ends 7.0.

Gill openings. Length 1st 1.3; 3rd 1.3; 5th 1.1; distance between inner ends 1st 15.5; 5th 7.6.

First dorsal fin. Height 2.6; length of base 4.2.

Second dorsal fin. Height 2.8; length of base 4.6.

Pelvics. Anterior margin 13.6.

Distance. From tip of snout to center of cloaca 42.7; from center of cloaca to 1st dorsal 44.7; to tip of tail 57.3; from rear end of 2nd dorsal base to tip of tail 3.8. Interspace 1st and 2nd dorsals 0.0.

Disc obtusely rounded in front, thence concave toward outer corners which are broadly rounded; posterior margin rounded;

maximum angle in front of spiracles 135°; width across anterior edge of orbits 28.5 per cent of total length of specimen. Axis of greatest breadth 75 per cent of distance rearward from tip of snout to axils of pectorals.

Thorns in the nuchal-scapular region in a triangular patch, continuing in a band of 5 rows along back, without interruption, and on to tail, where they are somewhat larger and in 5-6 rows anteriorly, thence narrowing to 2-3 rows, ending at first dorsal; anterior and inner margins of orbits with a row of 7 or 8 thorns, also a pair opposite each spiracle; a patch of prominent and sharp malar thorns opposite the spiracles and orbits, the length of patch about 70 mm and greatest width 20 mm; alars in as many as 4 rows, the longest row 70 mm; disc and tail covered with fine close-set prickles, coarsened in advance of the short triangular rostral process; prickles present on skin over eyes and on dorsal and caudal fins, also a few on posterior lobes of pelvics. Lower surface of disc and tail smooth.

The claspers extend from the axil of pelvics a distance a little greater than from tip of snout to rear margin of orbits.

Jaws strongly arched centrally. Teeth $\frac{37}{36}$, uppers in center of jaw crowded, with slender to narrowly triangular cusps, those toward corners of jaw arranged in parallel rows, not in quincunx; lowers similar, but those in median sector larger than corresponding upper teeth.

Color above plain medium brown, dorsals and caudal fins blackish; below, black except pale around jaws, on nasal flap, edges of gill openings, in areas near end of snout, and at tip of anterior pelvic lobes.

Cruriraja rugosa Bigelow and Schroeder 1958

This skate appears to be relatively common within its known geographic and depth ranges. We have previously recorded (1958, 1962, 1965) 103 specimens from numerous localities extending from the northern part of the Gulf of Mexico to the northern coast of Panama, the latter at 9°03′N, 81°18′W. These ranged in length from 90 to 485 mm and were trawled in depths of 200-500 fathoms (366-915 m).

The present collection includes 19 *rugosa* of 100-404 mm, from 250-550 fathoms (457-1007 m), taken at "Oregon" stations 4414, 4662, 4663, 4730, 4731, 4816, 4883, 4902, 5039, and "Silver Bay" station 5142. Most are from within the geographic range

given above, but included are four additional localities: (1) the north coast of Haiti, (2) the coast of Colombia, (3) southwest of Curaçao, and (4) southwest of Grenada at 11°40′N, 62°33′W.

Family PSEUDORAJIDAE

Pseudoraja atlantica Bigelow and Schroeder 1962

Many specimens of this species have been recorded (1962, 1965) from off the Atlantic coast of Nicaragua, 13°31′N, to the offing of the Amazon River, 01°45′N, in depths of 135-350 fathoms (247-640 m), in length 86-481 mm. The present collection includes 32 males and 22 females trawled at 25 "Oregon" stations from off the coast of Panama 9°47′N, 79°25′W to the vicinity of Tobago, 11°31′N, 60°51′W, in depths of 200-340 fathoms (366-622 m), in length 90-518 mm.

Mature males have a patch of malar thorns along the outer part of the pectorals from end of snout to a little in advance of a line through the orbits. These prominent thorns may have sharp tips or be covered by skin. A few may be present on individuals as small as 350 mm but in sizes upward of about 420 mm, they are well developed.

The alar thorns usually start to appear at about 400 mm. On a specimen of 425 mm they are in 2 to 3 rows, on one of 447 mm up to 6 rows, but on the largest male of 491 mm there are only 3 to 4 rows of thorns. The size of the patch of thorns ranges from about 40 to 48 mm in length and 9 to 12 mm in width, usually with but 1 or 2 thorns at the anterior and posterior ends.

The claspers on a 230 mm specimen are minute and do not reach the tip of the posterior pelvic lobe; at 340-400 mm they reach a little beyond the pelvic lobe and at maturity, when they have become rigid, they extend for a considerable distance.

Family ANACANTHOBATIDAE

Anacanthobatis americanus Bigelow and Schroeder 1962

Published accounts (1962, 1965) of this species include 51 specimens taken at 12 "Oregon" stations from off the coasts of British Guiana, Venezuela, Panama, and Honduras, 7°34′ to 16°35′N, in 100-400 fathoms (183-732 m), ranging in length from 95 to 350 mm. The present collection includes 42 specimens taken at 15 "Oregon" stations (4412, 4413, 4415, 4416, 4424, 4841, 4842, 4854, 4855, 4902, 4912, 4925, 5039, 5689, 5690) all from off the coasts of Colombia and Venezuela between 09°02′-12°30′N

and 76°31′-69°18′W, and "Silver Bay" station 5142 off the north coast of Haiti at 19°52′N, 71°58′W, in depths of 205-500 fathoms (375-915 m), in length 114-362 mm.

The size at which males reach maturity varies. Thus, on one of 270 mm the claspers are minute, and while one of 295 mm is mature, with rigid claspers, hooks exposed, pelvics and pectorals separated, another of 320 mm is immature, with flexible claspers and the pelvics and pectorals still united. The alars at maturity are in up to 5 rows, the patch of thorns on the largest male, of 350 mm, being 29 mm long and 10 mm wide.

Anacanthobatis longirostris Bigelow and Schroeder 1962

Three specimens of this bizarre skate have been recorded (1962, 1965): a female of 507 mm, the holotype, from off the Mississippi Delta, 29°09′N, 87°53′W, in 500-575 fathoms (915-1052 m), "Oregon" station 2823; a male of 135 mm from Santaren Channel, 23°59′N, 79°43′W, in 350 fathoms (640 m), "Combat" station 450; and an immature male of 483 mm from the same locality, 23°40′N, 79°13′W, in 290 fathoms (530 m), "Silver Bay" station 2458.

Two more have been trawled, both females, of 745 and 630 mm respectively, off the north coast of Haiti at 19°55′N, 72°00′W, in 470-500 fathoms (860-915 m), "Silver Bay" station 5146. Proportional dimensions in per cent of total length (exclusive of filament at tip of snout) of both specimens follow:

Disc. Extreme breadth 61.2, 56.3; length 74.3, 64.7.

Snout length. In front of orbits 33.0, 30.1; in front of mouth 35.5, 33.1.

Orbits. Horizontal diameter 2.8, 2.7; distance between 3.8, 2.9.

Spiracles. Length 1.6, 1.0; distance between 6.1, 5.7.

Mouth. Breadth 5.3, 5.1.

Exposed nostrils. Distance between inner ends 5.5, 4.9.

Gill openings. Length, 1st 1.0, 1.0; 3rd 1.0, 1.0; 5th 0.7, 0.8; distance between inner ends, 1st 11.6, 10.8; 5th 8.2, 7.3.

Pelvics. Length of anterior limb 15.3, 12.0; distance, origin of anterior limb to tip of posterior lobe 13.3, 13.2.

Distance. From tip of snout (from base of filament) to center of cloaca 61.7, 57.1; from center of cloaca to tip of tail 38.3, 42.9.

The axis of greatest breadth of the disc is about two-thirds the distance back from tip of snout to axils of pectorals. The upper caudal fin is vestigial on the 745 mm specimen and the lower caudal appears to be missing, while on the one of 630 mm the tip of tail is

lacking, total length having been estimated on the basis of the disc width. The proportional dimensions of the latter specimen agree closely with the holotype but the one of 745 mm has a longer snout, 33.0 per cent of total length of specimen; vertical length of disc, 74.3 per cent; wider disc, 61.2 per cent; and a greater distance from tip of snout to center of cloaca, 61.7 per cent, these proportions on the holotype being 29.8, 64.7, 56.8 and 57.4 per cent, respectively.

SPRINGERIA FOLIROSTRIS Bigelow and Schroeder 1951

Many specimens of this species have been recorded (Springer and Bullis, 1956; Bigelow and Schroeder, 1951a, 1965), all of them from the northern part of the Gulf of Mexico, ranging in latitude from 26°46′ to 29°30′N, in longitude from 85°09′ to 96°20′W, from depths of 164 to 280 fathoms (300-512 m), in length from 125 to 620 mm.

In our last account of *S. folirostris* a description was given of a male, of 576 mm, the first mature specimen to come to our attention. This showed that on males the posterior lobe of the pelvics ceases to be adnate to the pectorals when that stage of growth is attained, as occurs with *Anacanthobatis americanus.*

The present collection includes three females 140-330 mm long and a male of 195 mm, from 27°56′N, 90°36′W, in 220 fathoms (402 m), "Oregon" station 4704, also a nearly mature male of 530 mm from 27°45′N, 93°56′W, in 200 fathoms (366 m), station 4606.

Proportional dimensions in per cent of total length of the 530 mm male.

Disc. Extreme breadth 52.0; length 54.7.

Snout length. In front of orbits 21.0; in front of mouth 22.5.

Orbits. Horizontal diameter 3.4; distance between 2.2.

Spiracles. Length 1.0; distance between 5.5.

Mouth. Breadth 4.7.

Exposed nostrils. Distance between inner ends 4.5.

Gill openings. Length 1st 0.76; 3rd 0.76; 5th 0.66; distance between inner ends, 1st 9.5; 5th 4.9.

Caudal fin. Length of base, upper 4.7; lower 4.2.

Pelvics. Length of anterior limb 13.0; origin of anterior limb to tip of posterior lobe 11.0.

Distance. From tip of snout (from base of tentacle) to center of cloaca 47.5; from center of cloaca to tip of tail 52.5.

These proportions agree closely with those of the holotype, a male 400 mm long.

The pectorals and pelvics are free, as on a fully mature male. The claspers, which are semi-flexible and with the hooks not yet exposed, extend beyond the tips of the pelvics a distance equal to the space between the outer margins of the spiracles. The alar thorns have broken through the skin but are not fully developed, the greatest width and length of the patch, on each side, being 12 mm and 25 mm, respectively, with the thorns arranged in as many as 4 rows. The jaws are rather strongly arched. Teeth $\frac{2}{2}\frac{9}{7}$, those in center of jaw the smallest and more crowded, with a triangular blunted cusp, those toward corners of jaw with a flat crown.

Grayish brown above, whitish below, except for some brownish blotches on the posterior segment of the pelvic limb and a broad band of pale gray along the outer margin of the disc.

ADDENDUM

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Diplobatis pictus . . . . . 1962, pl. 1
Raja bullisi . . . . . 1962, fig. 1
Raja cervigoni . . . . . 1964, fig. 1
Raja clarkii . . . . . 1958, fig. 8; 1965, fig. 1
Raja floridana . . . . . 1962, figs. 2, 3
Raja fuliginea . . . . . 1954, fig. 4
Raja lentiginosa . . . . . 1951b, fig. 1; 1953, fig. 48a
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CAMBRIDGE, MASS. 5 APRIL, 1968 NUMBER 282

THE EXTINCT BABOON, *PARAPAPIO JONESI*, IN THE EARLY PLEISTOCENE OF NORTHWESTERN KENYA

Bryan Patterson

Among the fossils collected during 1966 in the early Pleistocene sediments of the Kanapoi area, southeastern Turkana (Patterson, 1966), is a specimen of a small baboon. The surface find of a fragment of a right horizontal ramus with M_{2-3} prompted excavation at the spot and sifting of the slope debris. No parts were found *in situ* but a number of fragments were recovered from the slope and several of these fitted together to form a partial mandible. Good contacts are present from the symphysis back to the base of the ascending ramus on the right side. The bases of the incisors and canines and the anterior root of the right P_3 are preserved in the symphysis; complete or nearly complete teeth present are the left P_4, M_1 and M_3 and the right M_{2-3}. The specimen bears the field number 122-66K, and was found by Mr. Roger C. Wood in the drainage of the Kikimon, a dry wash east of the Kanapoi and, like it, draining into the Kakuryo. All fragments were found within a small area, which, together with the gentle nature of the slope, suggests that the fossil may not have moved far from its burial place.

As is shown by the sizes of the incisors and canines relative to the cheek teeth and by the marked overlap of the anterior root of P_3 along the posterolateral face of the canine, the specimen is certainly a male. It agrees so closely with specimens of *Parapapio jonesi* Broom from South Africa that, if Freedman's (1957, 1960) specific distinctions are accepted, there can be no doubt as to the identification.

Freedman has discussed the structure of this and other species of *Parapapio* in considerable detail, which makes it unnecessary to do more than comment on a few points. Curiously enough, the new specimen has the most complete symphysis of any male individual

of *P. jonesi* yet collected. The anterior surface is not steep, forming an angle of approximately 45° with the lower border of the horizontal ramus. The two ridges that converge upward toward each of the median incisors are not very prominent; they enclose a shallow, median depressed area that extends dorsally from the foramen symphyseosum. Between the posterior portion of the ridge, below, and the anterior alveolus of P_3, above, is a small,

Fig. 1. *Parapapio jonesi* Broom. Field no. 122-66K. Dorsal view of incomplete mandible of male. ×1.

rather rugose depression. Apart from this, the anterior surface is only slightly roughened. The incisal shelf slopes very gently downward from the incisor alveoli to a point opposite about the middle of P_3. The symphysis terminates at the level of the anterior end of P_4; there is no mental spine. The ascending ramus arises a little

behind M_3. The lateral face of the horizontal ramus is very slightly concave beneath M_2 and the anterior half of M_3, but neither here nor in the portion of the bone beneath the left P_4 — M_1 is there any delimitation of a mandibular fossa as such. The teeth preserved call for no special comment.

Measurements (in mm)

	C	P_4	M_1	M_2	M_3
Length (mesio-distal)	6.3	6.4	8.2	10.4	12.7
Width	10.0	6.2+			
Width, anterior			7.3	8.8+	9.6
Width, posterior			7.1	9.1	8.6
Width, hypoconulid					5.0
Depth of ramus posterior to M_3	29.1				

All measurements have been taken in accordance with Freedman's methods. Dimensions of the Kanapoi specimen fall, or, in the case of the widths of P_4 and M_2, presumably fell, within the observed ranges for males of his sample of *P. jonesi* (1957, tables 6b, 6d) in all cases but three. These, the anterior and posterior widths of M_1 and the length of M_3, fall within the observed ranges for females. As he stresses, the ranges of the two sexes overlap broadly for P_4 — M_3 in the genus. His samples for males, furthermore, are small, numbering only 5, 4 and 3 in these cases.

Parapapio is characteristic of the older part of the South African Pleistocene sequence. *P. jonesi* is well represented at Sterkfontein

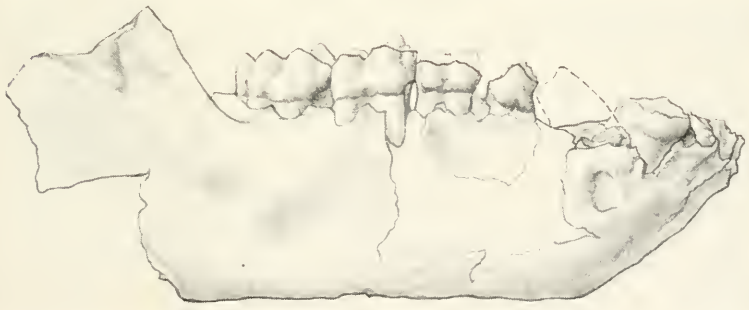

Figure 2. *Parapapio jonesi* Broom. Field no. 122-66K. Right lateral view of incomplete mandible of male. The ramus fragment with P_4 — M_3 has been reversed from the left side. ×1.

and Makapan, by 24 and 15 specimens, respectively, and one individual from Taung has been referred to it. The only specimens of *Parapapio* recorded from Swartkrans and Kromdraai are five individuals, 3 and 2, respectively, of a small form, and these are fragmentary. Freedman placed them with some hesitation in *P. jonesi*, pointing out that better material might in future require their separation. Two partial female mandibles from Swartkrans have "fairly large and quite deep mandibular fossae," a feature conspicuously lacking in those from the earlier deposits. The Kanapoi specimen agrees with the earlier South African material and adds one more to the small list of species in common between the early Pleistocene of eastern and southern Africa.

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SCYTHIAN AMMONOIDS FROM TIMOR

Bernhard Kummel

One of the more important areas of ammonitiferous Scythian (Lower Triassic) strata is the island of Timor. The monograph by Welter (1922) on the Lower Triassic ammonoids of Timor is the standard reference. However, an earlier paper by Wanner (1911) did describe four species of Lower Triassic ammonoids. A number of additional comments and descriptions on these Timor ammonoids were contributed by Spath (1934). In the course of a general study of all Scythian ammonoids I have had the opportunity to examine many collections from Timor including the type specimens of the Wanner (1911) and Welter (1922) studies. This note was prepared to make some additions and corrections to our knowledge of Scythian ammonoids of Timor.

Prosphingites austini Hyatt and Smith is recorded for the first time from Timor. This is a common species of *Owenites* Zone age in the circum-Pacific and Arctic regions.

Prenkites sundaicus Welter is established as the type of a new genus, *Vickohlerites*. Previous problems in the interpretation of this species were due to the inaccurate suture illustrated by Welter (1922).

The genus *Parowenites* Spath (1934) was established for an owenitid with a presumed goniatitic suture as illustrated by Welter (1922, pl. 169 (15), figs. 5, 8). Examination of Welter's types clearly shows that the goniatitic suture is the result of excessive grinding and polishing of the specimens. Preparation of other paratypes shows that the suture is ceratitic; hence the genus *Parowenites* Spath is a synonym of *Owenites* Hyatt and Smith.

The genus *Metadagnoceras* Tozer is recognized for the first time from the bed with manganese coated fossils at Nifoekoko. This specimen had previously been noted by Spath (1934, p. 269, footnote) as being "very close to *Dagnoceras terbunicum*."

For the loan of specimens used in this study I am very grateful to Dr. H.K. Erben of Bonn University, Dr. M.K. Howarth of the British Museum (Natural History), and Dr. H.J. MacGillavry of the Geological Institute, Amsterdam University. The laboratory aspects of this study were supported by N.S.F. grant GB-5109X.

SYSTEMATIC PALEONTOLOGY

Class CEPHALOPODA Cuvier, 1797
Subclass AMMONOIDEA Zittel, 1884
Family PROPTYCHITIDAE Waagen, 1895
Genus OWENITES Hyatt and Smith, 1905
Type species, *Owenites koeneni* Hyatt and Smith, 1905

OWENITES SIMPLEX Welter

Plate 1, figures 1-9

Owenites simplex Welter, 1922: 153, pl. 169(15), figs. 1-8; Kutassy, 1933: 606.

Parowenites simplex, — Spath, 1934: 187, fig. 58; Kummel *in* Arkell *et al.*, 1957: L138, figs. 171-1a,b; Kummel and Steele, 1962: 647.

Owenites kwangsiensis Chao, 1959: 83, 250, pl. 22, figs. 1-6, text-fig. 26b.

Owenites plicatus Chao, 1959: 85, 251, pl. 22, figs. 19-21, text-fig. 26e.

Owenites aff. *plicatus* Chao, 1959: pl. 22, figs. 24, 25.

Owenites costatus Chao, 1959: 83, 249, pl. 22, figs. 10-18, 22, 23, text-fig. 26c.

Owenites costatus var. *lenticularis* Chao, 1959: 84, 249, pl. 22, figs. 7-9, text-fig. 26d.

Spath (1934: 187) established the genus *Parowenites* primarily on the basis of the goniatitic suture of *Owenites simplex* as reproduced by Welter (1922: pl. 169(15), figs. 5, 8). Examination of Welter's type specimens plus a number of paratypes shows that the sutures reproduced by Welter were exposed by grinding and polishing. The specimen which yielded the suture of Welter's figure 8 is apparently lost, as it is not in the collections of the Paleontological Institute, Bonn University.[1] However, the paratype of Welter's plate 169(15), figures 3-5 is available, and this shows clearly that excessive grinding of the lateral area resulted in the simple, goniatitic suture. One of the unfigured paratypes of Welter (Pl. 1,

[1] Abbreviations in this paper: MCZ = Museum of Comparative Zoology; GPIBo = Geologisch-Paläontologisches Institut, Bonn; BMNH = British Museum (Natural History).

figs. 8, 9 of this report) yielded the suture of Figure 3E. As can readily be seen, the two lateral lobes are ceratitic and the whole aspect of the suture is owenitid.

The measurements of 27 specimens of this species are given on Table I, and plotted on the graph of Figure 1. There is considerable variation in the diameter of the umbilicus which interestingly enough is not obvious on casual inspection of the specimens. What is more interesting is that the diameter of the umbilicus can vary from one side of the conch to the other. For instance, one of the paralectotypes (Pl. 1, figs. 3-5) has an umbilical diameter of 3.7 mm on one side and 4.6 mm on the other side of the conch.

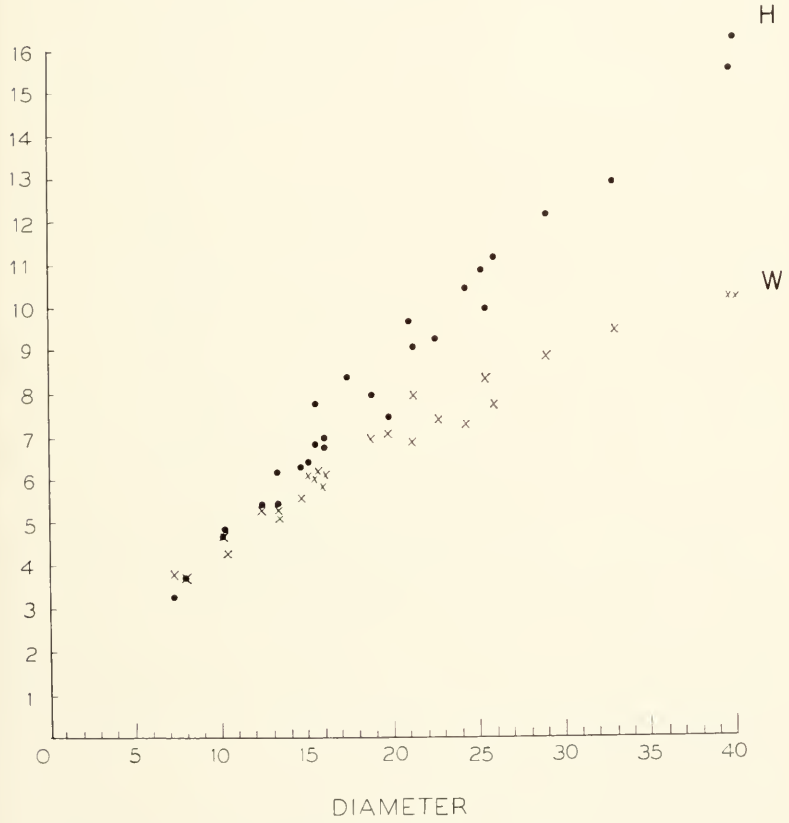

Figure 1. Variation in whorl height (H) and whorl width (W) of *Owenites simplex* from limestone blocks with *Owenites egrediens*, Bahati, Timor.

The form described by Chao (1959) as *Owenites kwangsiensis* from the *Owenites* Zone of Kwangsi, China, I consider to be identical to *O. simplex* Welter (Figs. 3E, H). From the same horizon and locality which yielded *Owenites kwangsiensis,* Chao (1959) described *O. costatus* and *O. plicatus.* Of the first of these species Chao had 17 specimens which he compared mainly with *Owenites pakungensis* Chao; the latter I consider a synonym of *Owenites koeneni* (Kummel and Erben, 1968). *Owenites costatus* does have constrictions and ribs but these are stated to be developed on an irregular pattern, thus differentiated from *Owenites kwangsiensis.* Examination of the 31 specimens from Timor of *Owenites simplex,* representing all growth stages, shows that there is great variation in the pattern of ornamentation. Every one of the specimens of *Owenites costatus* illustrated by Chao (1959: pl. 22, figs. 10-18, 22, 23) can be directly compared to one of the Timor specimens before me. *Owenites plicatus* Chao was established on two fragmentary specimens. On the basis of the description and illustrations of these two specimens I can see no reason for separating them from *O. simplex.* The apparently more simplified suture (fig. 21) was noted by Chao as most probably reflecting immaturity and not a distinctive new pattern. Owenitids of the type of *O. simplex* are only known from Timor and Kwangsi, China.

Occurrence — Dark red limestone blocks with *Owenites egrediens* of Bahati, Timor.

Repository — All specimens are in the Paleontological Institute, Bonn University.

Family PARANANNITIDAE Spath, 1930

Genus PROSPHINGITES Mojsisovics, 1886

Type species, *Prosphingites czekanowskii* Mojsisovics, 1886

PROSPHINGITES AUSTINI Hyatt and Smith

Plate 2, figures 1-16

Prosphingites austini Hyatt and Smith, 1905: 72, pl. 7, figs. 1-4; Frech, 1908, pl. 63, fig. 5; Krafft and Diener, 1909: 160; Diener, 1915: 233; Smith, 1932: 98, pl. 7, figs. 1-4; Spath, 1934: 195-196; Kummel and Steele, 1962: 683; Kummel, 1965: 544.

Prosphingites sp. indet. Spath, 1921: 298, 301.

Prosphingites spathi Frebold, 1930: 20, pl. 4, figs. 2, 3, 3a; Spath, 1934: 195, pl. 13, figs. 1, 2; Tozer, 1961: 58, pl. 13, figs. 1, 2; Kummel and Steele, 1962: 687; Kummel, 1965: 544.

Prosphingites sinensis Chao, 1959: 122, 297, pl. 25, figs. 1-5, pl. 27, figs. 1-17, text-figs. 40a-c; Kummel, 1965: 544.

Prosphingites radians Chao, 1959: 123, 298, pl. 28, figs. 12-16, text-fig. 39d; Kummel, 1965: 544.

Prosphingites ovalis Kiparisova, 1960: 137, pl. 33, figs. 2-4; Kiparisova, 1961: 115, pl. 25, figs. 6-9.

Prosphingites orientalis Kiparisova, 1961: 117, pl. 26, figs. 1, 2.

Prosphingites slossi Kummel and Steele, 1962: 683, pl. 101, figs. 8-17; Kummel, 1965: 544.

None of the three previous studies on Scythian ammonoids from Timor (Wanner, 1911; Welter, 1922; Spath, 1934) contains any mention of the genus *Prosphingites*. I have available five specimens that can with confidence be assigned to *Prosphingites austini* Hyatt and Smith. These specimens are from Fatoe Kosat and are part of the Jonker Collection of the Geological Institute, Amsterdam University. Measurements (in mm) on four of these species are as follows:

D	W	H	U
34.5	21.7 ?	13.3	11.8
30.8	16.7	13.6	8.4
27.8	?	12.8	7.8
27.2 ?	17.0	11.3	8.2
26.0	18.5	12.3	8.2

The similarity of these Timor specimens with *Prosphingites slossi* Kummel and Steele (1962: 683, pl. 101, figs. 8-17) and other mid-Scythian prosphingitids is indeed remarkable (Pl. 2). Documentation of species of this genus has been slow. The genotype (*P. czekanowskii* Mojsisovics, 1886) is from northern Siberia and of late Scythian age. Hyatt and Smith (1905) then described *Prosphingites austini* from the *Meekoceras* beds of the Inyo Range, southeastern California. Frebold (1930) and Spath (1934) recorded the Spitsbergen species — *Prosphingites spathi* — which they considered late Scythian in age. It was not until the post-war period that descriptions of a number of new species from middle and late Scythian horizons began to appear. These were from Scythian faunas of the Primorye Region (Kiparisova, 1961), southern China (Chao, 1959), New Zealand (Kummel, 1965), and Nevada (Kummel and Steele, 1962). From the mid-Scythian, *Owenites* Zone, the following species of *Prosphingites* are known: *Prosphingites austini* Hyatt and Smith, *P. ovalis* Kiparisova, *P.*

orientalis Kiparisova, *P. sinensis* Chao, *P. involutus* Chao, *P. kwangsianus* Chao, *P. radians* Chao, *P. spathi* Frebold, and *P. slossi* Kummel and Steele. Most of these species were introduced over a short period of time (1959-1962) and each author was generally without knowledge of the others' activities. We thus have an accumulation of species in which very little comparative analysis accompanied their original descriptions.

When I introduced the species *Prosphingites slossi* (Kummel and Steele, 1962) I was fully cognizant of its close relationship and possible identity to *P. austini* Hyatt and Smith (Pl. 2, figs. 1-3); however, on the argument that *Prosphingites austini* was known only from a single and not a very well preserved specimen, I considered it best to ignore the species. However, subsequently, on study of all new Scythian species that had been introduced, and through restudy of *P. austini,* I am now convinced that *P. slossi* is a synonym of *P. austini.* Kummel and Steele (1962) presented measurements on 49 specimens of *P. slossi* from the *Meekoceras* beds at Crittenden Spring, Nevada. These data show that at least within that population there is considerable variability in conch width and umbilical diameter. This collection also clearly showed that there was considerable variation in the pattern of constrictions.

Of the Timor specimens recorded here, only four yielded complete measurements. The range of umbilical diameters in these four specimens falls well within the range of umbilical diameters in the Crittenden Spring fauna of *Prosphingites slossi.* The whorl width tends, however, to be greater in the Timor forms than in the Nevada fauna. This, however, considering the small size of the sample and the identity or close similarity of the other conch features, is not sufficient reason to even suggest specific distinction. The pattern of ornament, and variations in the nature of the umbilical shoulder and wall are the same. The sutures can be said to be identical (Fig. 2).

Most of the other species placed here in the synonymy of *Prosphingites austini* are known from very few specimens. Large numbers of specimens of *P. spathi* are in the British Museum (Natural History), but only a few measurements are available and nearly all of this Spitsbergen collection consists of small phragmocones or juvenile specimens. It is uncertain from the text but it appears that the fauna of *Prosphingites spathi* from Ellesmere Island studied by Tozer (1961) consists of very few specimens, perhaps only three. Both Spath (1934) and Tozer (1961) have emphasized the variability of this species, including its suture. I can find no criteria by

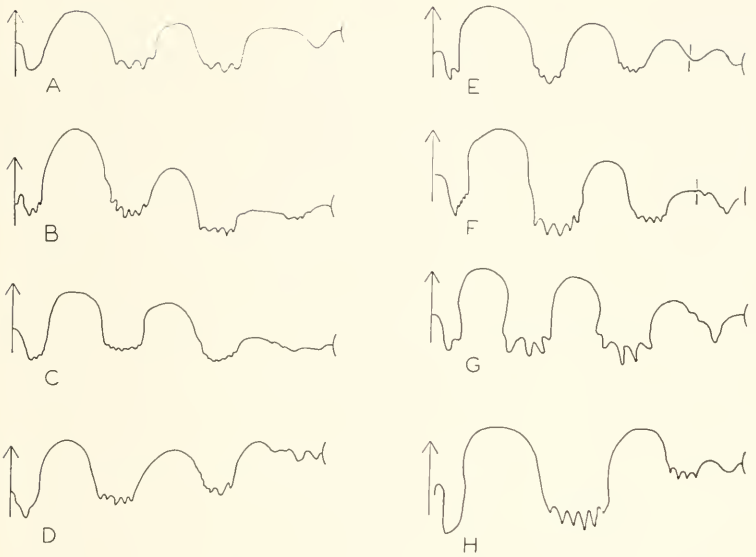

Figure 2. Diagrammatic representation of the suture of: A, *Prosphingites austini* Hyatt and Smith (1905: pl. 7, fig. 4) from *Meekoceras* beds, Union Wash, Inyo County, California, USNM 75256, at a diameter of 20 mm; B, *Prosphingites slossi* Kummel and Steele, from *Meekoceras* beds, Crittenden Spring, Nevada, paratype, at diameter of 18 mm; C, *Prosphingites slossi* Kummel and Steele, from *Meekoceras* beds, Crittenden Spring, Nevada, paratype, at a diameter of 30 mm; D, *Prosphingites spathi* Frebold, from Tozer (1961: pl. 13, fig. 1c) from *Meekoceras* beds, Blind Fiord Formation, Ellesmere Island, at a diameter of 16 mm; E, *Prosphingites spathi* Frebold, from Spath (1934: pl. 13, fig. 1e) from *Owenites* Zone, Spitsbergen; F, *Prosphingites austini* Hyatt and Smith, specimen in Yonker collection, from Timor, Department of Geology, Amsterdam University, at a diameter of 22 mm; G, *Prosphingites ovalis* Kiparisova (1961: fig. 79) from *Owenites* Zone, Primorye Region, at a whorl height of 5 mm; H, *Prosphingites sinensis* Chao (1959: fig. 40a) from *Owenites* Zone, Kwangsi, China, at a diameter of 20 mm.

which one can separate *P. spathi* from *P. austini.* In regards to the age of the Spitsbergen forms it has been pointed out by Kummel (1961) and Tozer (1961) that the beds containing *P. spathi* are of mid-Scythian *Owenites* Zone age rather than late Scythian as believed by Spath.

The mid-Scythian, *Owenites* Zone, strata of the Primorye Region contain, according to L. D. Kiparisova (1961), two species of

Prosphingites, namely, P. *ovalis* Kiparisova and P. *orientalis* Kiparisova. The first of these species, *P. ovalis*, was said to differ from *P. spathi* in its larger shell, oval coiling, more denticulated lobes, and narrower ventral saddle. On close examination none of these criteria are valid. The Arctic *P. spathi* so far is known from very few specimens on Ellesmere Island and several but mainly juvenile forms from Spitsbergen. Even so, size is hardly a parameter for species distinction, especially in a case like this. In regards to the suture, an inspection of Figure 2 demonstrates considerable variability in this respect. The Crittenden Spring fauna also shows considerable variability in details of the suture. The same variability has been noted for *P. spathi* by Spath (1934) and Tozer (1961). Authors continue to place too high a degree of importance on minor variations in suture patterns. Time and trouble generally dictate the representation in a description of only one suture pattern. My own experience has amply shown that the suture is as variable as any other conch feature in most if not all Scythian ammonoids.

From the same horizon and locality in the Primorye Region, Kiparisova (1961) has described *Prosphingites orientalis*. From the two illustrations given by Kiparisova (1961: pl. 26, figs 1, 2), *P. orientalis* differs from *P. ovalis* primarily in the more acute rounding of the umbilical shoulder. The contrast in the nature of the umbilical shoulder of these two species is precisely the same as seen in the fauna of *Prosphingites slossi* from Crittenden Spring, Nevada (Kummel and Steele, 1962: pl. 104, figs. 8-17). The supposed ovate coiling of *P. ovalis* is suspect, as not all of the illustrated specimens show this. Even so, variants showing slightly ovate coiling are common in Scythian ammonoids. Again, I can see nothing in the suture, conch shape or pattern of constrictions in these Primorye forms to separate them from *P. austini*, *P. slossi*, or *P. spathi*.

Among the very large Scythian fauna of Kwangsi, China, Chao (1959) recognized a number of prosphingitids. Among these, *Prosphingites radians* must be considered a synonym of *P. austini* and the other species discussed above. The conch form, pattern of constrictions and suture (Fig. 2) are well within the range of variation of what is here defined as *P. austini*. There is, in addition, *Prosphingites sinensis*, of which I am not as confident in placing in the synonymy of *P. austini*. The description and illustrations of this species leave much to be desired. However, on the basis of available data, I consider it most probable that this species is the same

as *P. austini*. Even the unusual suture, in terms of the other forms combined with *P. austini*, may not be definitive (Fig. 2H).

Prosphingites kwangsianus Chao (1959: 296, pl. 28, figs. 17-22) is reported to be a smooth form lacking constrictions. The species, however, is based on two incomplete specimens of modest preservation. More satisfactory documentation of this species I suspect would show it to be conspecific with all the forms placed here in *Prosphingites austini*.

Occurrence. — The Timor specimens recorded here are from red limestones at Fatoe Kosat, Timor.

Repository. — Collection of Lower Triassic ammonoids made by Dr. H. G. Jonker during his Timor expedition in 1915-1916. Specimens are deposited in the Timor collection of the Geological Institute, University of Amsterdam.

Genus Vickohlerites n.g.

Type species, *Prenkites sundaicus* Welter, 1922

Conch evolute, with depressed whorl section, broad rounded venter, conch smooth except for growth lines. Suture consists of two denticulated lateral lobes and an auxiliary lobe on the umbilical wall. The type species is from an unknown horizon on Timor. Conspecific specimens are present in the *Subcolumbites* fauna of Chios and an indeterminant species (but not conspecific) is present in the *Subcolumbites* fauna of Kotal-e-Tera, Afghanistan (Kummel, 1968).

Vickohlerites sundaicus (Welter)

Plate 1, figures 10, 11

Prenkites sundaicus Welter, 1922: 150, pl. 168 (14), figs. 18-21; Kutassy, 1933: 621; C. Renz, 1945: 301; Renz and Renz, 1947: 60; Renz and Renz, 1948: 29, pl. 12, fig. 1; Chao, 1959: 306.

"Prenkites" sundaicus, — Spath, 1930: 77; Spath, 1934: 188, 209.

Welter (1922) described this species on the basis of a single specimen from Noel Niti, Timor, and was quite positive as to the close relationship of his specimen to *Prenkites malsorensis* Arthaber from the *Subcolumbites* fauna of Albania. This close relationship is difficult to see. *Prenkites* is a more involute form, with depressed whorls which contract on the adoral quarter volution. The umbilical shoulders are subangular and bear fine nodes. The Timor specimen has a diameter of 40.7 mm, an adoral whorl of 21.5 mm, a height of the adoral whorl of 13.2 mm and an umbilical diameter

of 20.3 mm. The conch is evolute, the umbilicus comprising approximately 50 per cent of the conch diameter. The whorls are depressed with the maximum width at the umbilical shoulder. The venter is arched and grades with no perceptible ventral shoulder to the umbilical shoulder which is acutely rounded. The umbilical wall is steep but not vertical. The last half volution of the specimens is body chamber and shows traces of delicate growth lines. The penultimate half volution bears a series of weak forward projecting ridges which are most prominent on the center part of the venter and disappear completely midway between the venter and the umbilical shoulder.

It is in Welter's (1922: pl. 14, fig. 21) representation of the suture that one can pinpoint the uncertainty in interpretation of this form. Welter's drawing of the suture covers only the portion from the venter to the umbilical shoulder, but implied that is was a complete suture. A new drawing of the suture is given on Figure 3J. As can be seen, there are two prominent lateral lobes but the umbilical wall bears a good portion of a fairly large auxiliary saddle and a small but very distinct denticulated lateral lobe. The first author to comment on *Prenkites sundaicus* after Welter was Spath (1930: 77) who remarked " *'Prenkites' sundaicus* Welter, in whorl shape resembles *Columbites,* but in suture line it is closer to *Subcolumbites* . . ." In terms of Welter's representation of the suture this statement is correct. In *Columbites* the second lateral lobe is generally very small consisting of a single prong, whereas in *Subcolumbites* the second lateral lobe, though much smaller than the first, is more highly developed in terms of its breadth and pattern of denticulation. On the basis of suture alone, *Prenkites sundaicus* can not be attached to either *Columbites* or *Subcolumbites.*

There is a general similarity in conch shape of *Prenkites sundaicus* with some groups of *Subcolumbites.* Among the subcolumbitids three distinct groups can be recognized. There is first of all the *perrinismithi* group with a tendency for carination of the venter; secondly, the *dusmani* group with a more marked development of the reticulate ornamentation, and a compressed whorl section, but lacking the tendency toward carination; finally, there is the *robustus-multiformis* group characterized mainly by their depressed whorl section. It is to this last group that *Vickohlerites sundaicus* has great resemblance in conch form. Within the two subfamilies of the Paranannitidae those genera assigned to the Columbitinae tend to have sutures lacking an auxiliary lobe, whereas within the

Paranannitinae an auxiliary lobe is commonplace, as in *Prosphingites, Zenoites, Chiotites,* etc. It is within this subfamily that *Vickohlerites sundaicus* belongs.

Renz and Renz (1948: 24, pl. 12, fig. 1) have described and illustrated a single specimen from the *Subcolumbites* fauna of Chios as a representative of this species. The general conch form of their specimen is the same as that of the type specimens from Timor. This Chios specimen measures 55.5 mm in diameter, 21.4 mm for the width of the adoral whorl, 19 mm for the height, and 23.5 mm for the width of the umbilicus. The dimensions of the whorl height and umbilical diameter in the two specimens are reasonably similar. However, the Timor specimen has a broader whorl than the Chios specimen by approximately 14 per cent. This difference in whorl width is difficult to evaluate, as each locality has yielded only a single specimen. In addition, the Chios specimen, apparently, does not show the suture. The overall similarity of the Chios specimen to that from Timor is such that, in spite of the differences and lack of data mentioned above, the two specimens should be considered as conspecific.

An undescribed specimen from a *Subcolumbites* fauna at Kotal-e-Tera, Afghanistan, is clearly congeneric with the Timor and Chios specimens discussed above but is not conspecific. There are significant differences in whorl cross-section and in the suture.

Occurrence. — The holotype (Pl. 1, figs. 10, 11) is from Noel Niti, Timor. Welter (1922: 85, 86) considered this specimen to come from his lowest Triassic horizon. He lists (on p. 150) the forms associated with this specimen as *Meekoceras* sp. indet. The available evidence does not allow any precise determination of the age, but the biological affinities of this species suggest that it is late Scythian in age.

Repository. — The holotype is in the Paleontological Institute of Bonn University; the specimen from Chios is in the Natural History Museum, Basel J 13576.

Family MEEKOCERATIDAE Waagen, 1895

Genus METADAGNOCERAS Tozer, 1965

Type species, *Metadagnoceras pulcher* Tozer

METADAGNOCERAS FREEMANI n. sp.

Plate 1, figures 12, 13.

This species is proposed for the specimen from Timor mentioned by Spath (1934: 269, footnote) as "an isolated example of a new

species from Timor . . . which is very close to *Dagnoceras terbunicum.*" The specimen measures 47.8 mm in diameter, 14.7 mm for the width of the last whorl, 21.7 mm for the height of the last whorl, and 10.4 mm for the diameter of the umbilicus. The conch is compressed with a low, arched venter and rounded ventral and umbilical shoulders. The suture (Fig. 3D) has a very large first lateral lobe with denticulations extending all along the vertical side to a narrow irregular first lateral saddle. There is a small denticulated second lateral lobe on the umbilical shoulder and wall.

This species does not resemble *Dagnoceras terbunicum* in conch shape; the differences are centered mainly in the character of the venter. In the suture, the first lateral saddle and the first lateral lobe of the two species are quite similar but the remainder of the suture is quite different. In general conch morphology *Metadagnoceras freemani* is quite similar to the type species, *M. pulcher* Tozer. The sutures are similar in basic plan but differ in significant details (Figs. 3A, D). The suture is quite similar to an undescribed species from the Tobin Formation, Nevada, but the whorls are of quite different proportions and the conch much more evolute (Fig. 3B).

Occurrence. — Nifoekoko, Timor, from bed with manganese coated fossils, including *Albanites, Prohungarites,* etc.

Repository. — British Museum (Natural History) C33701, holotype.

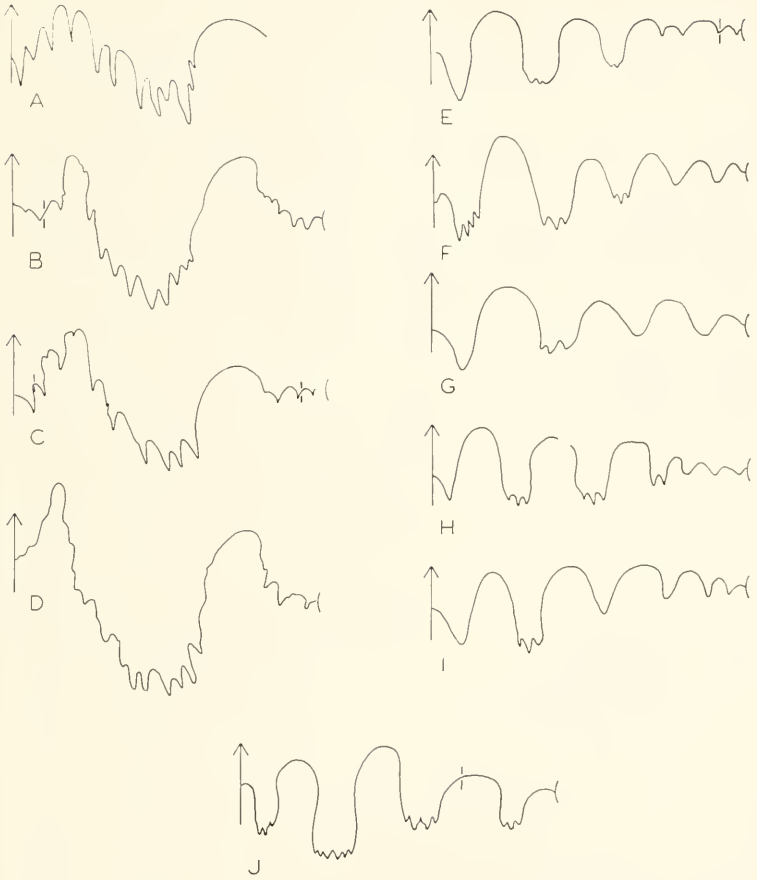

Figure 3. Diagrammatic representation of the suture of: A, *Metadagnoceras pulcher* Tozer (1965: fig. 9), from British Columbia, at a whorl height of approximately 20 mm; B, undescribed new species from Tobin Formation, Nevada, at a whorl height of 11 mm, MCZ 9638; C, undescribed species of *Metadagnoceras* collected by N. J. Silberling from Star Peak Formation, Nevada, at a whorl height of 22 mm; D, *Metadagnoceras freemani* n. sp., holotype, from Nifoekoko, Timor, at a whorl height of 14 mm, BMNH C33701; E, *Owenites simplex* Welter, original drawing based on one of Welter's unfigured paratypes (Pl. 1, figs. 8, 9 of this report) at a diameter of 13 mm; F, *Owenites costatus* Chao (1959: fig. 26c) at a diameter of 20 mm; G *Owenites costatus* var. *lenticularis* Chao (1959: fig. 26d) at a diameter of 12 mm; H, *Owenites kwangsiensis* Chao (1959: fig. 26b) at a diameter of 25 mm; I, *Owenites plicatus* Chao (1959: fig. 26e) at a diameter of 30 mm; J, *Vickohlerites sundaicus* (Welter), at a diameter of 30 mm, holotype, GPIBo 231.

TABLE 1

Measurements of *Owenites simplex* Welter from Timor

No.	D	W	H	U	W/D	H/D	U/D
1.	39.8	10.3	16.4	10.0	25.9	41.2	25.1
2.	39.6	10.3	15.6	7.2	26.0	39.3	18.2
3.	32.8	9.5?	13.0	13.4	28.9?	39.6	40.8
4.	28.9	8.9	12.2	7.2	30.8	42.2	24.9
5.	25.9	7.8	11.2	6.3?	30.1	43.2	24.3?
6.	25.4	8.4	10.0	8.0	33.1	39.4	31.4
7.	25.1	?	10.9	6.3	?	43.4	25.1
8.	24.2	7.3	10.5	5.8	30.2	43.4	23.9
9.	22.6	7.4	9.3	5.1	32.7	41.2	22.6
10.	21.2	8.0	9.1	5.6	37.7	42.9	26.4
11.	21.1	6.9	9.7?	4.9?	32.7	45.9?	23.2?
12.	19.7	7.1	7.5	6.2	36.0	38.1	31.5
13.	18.8	7.0	8.0	4.0	37.2	42.6	21.3
14.	17.4	?	8.4	3.1?	?	48.3	17.8?
15.	16.1	6.1	7.0	3.8	37.9	43.5	23.6
16.	16.0	5.9	6.8	4.6	36.9	42.5	28.8
17.	15.6	6.2?	6.8	3.8	39.7?	43.6	24.4
18.	15.5	6.1	7.8	4.0	39.4	50.3	25.8
19.	15.1	6.1	6.4	3.7	40.4	42.4	24.5
20.	13.3	5.3	6.2	2.7	39.8	46.6	20.3
21.	13.3	5.1	5.4	3.3	38.3	40.6	24.8
22.	14.6	5.6?	6.3	3.7	38.4?	43.2	25.3
23.	12.4	5.3	5.4	?	42.7	43.5	?
24.	10.4	4.3	4.8	1.6?	41.3	46.2	15.4?
25.	10.1	4.7	4.7	1.5?	46.5	46.5	14.9?
26.	8.0	3.7	3.7	?	46.3	46.3	?
27.	7.3	3.8	3.3	1.1?	52.1	45.2	15.1?

D = diameter; W = width of adoral whorl; H = height of adoral whorl; U = diameter of umbilicus.

No. 2. Lectotype, Welter (1922: pl. 169(15), figs. 1, 2; Pl. 1, figs. 1, 2 of this report) GPIBo 234a.

No. 8. Paralectotype, Welter (1922: pl. 169(15), figs. 3-5; Pl. 1, figs 3-5 of this report) GPIBo 234b.

No. 10. Paralectotype, Welter (1922: pl. 169(15), figs. 6, 7; Pl. 1, figs. 6, 7 of this report) GPIBo 234c.

No. 20. Suture specimen from Bahati, Timor (Pl. 1, figs. 8, 9, Text-fig. 3E of this report) GPIBo.

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EXPLANATION OF PLATE 1

Figs. 1-9. *Owenites simplex* Welter from Timor. Figs. 1, 2, lectotype (Welter, 1922: pl. 169(15), figs. 1, 2) GPIBo 234a, X1; 3-5 paralectotype (Welter, 1922: pl. 169(15), figs. 3-5) GPIBo 234b, X1.5; 6, 7, paralectotype (Welter, 1922: pl. 169(15), figs. 6, 7) GPIBo 234c, X1.5; 8, 9, paralectotype from which suture of Text-figure 3E was taken, GPIBo, X3.

Figs. 10, 11. *Vickohlerites sundaicus* (Welter) from unknown horizon on Timor. Holotype GPIBo 231, X1.

Figs. 12, 13. *Metadagnoceras freemani* n. sp. from beds with managanese coated fossils, Nifoekoko, Timor. Holotype, BMNH C33701, X1.

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EXPLANATION OF PLATE 2

Figs. 1-16. *Prosphingites austini* Hyatt and Smith. Figs. 1-3, from *Meekoceras* beds Union Wash, Inyo Range, California, holotype USNM 75256, X1.5; 3, 4, *Prosphingites slossi* Kummel and Steele, from *Meekoceras* beds, Crittenden Spring, Nevada, paratype MCZ 5781, X1; 6, 7, *Prosphingites slossi* Kummel and Steele from *Meekoceras* beds, Crittenden Spring, Nevada, paratype MCZ 5616, X1; 8, *Prosphingites slossi* Kummel and Steele from *Meekoceras* beds, Crittenden Spring, Nevada, paratype MCZ 5615 X1; 9, 10, *Prosphingites slossi* Kummel and Steele, from *Meekoceras* beds, Crittenden Spring, Nevada, holotype MCZ 5614, X1; 11-16, *Prosphingites austini,* Jonker Collection, Timor, Geology Department, University of Amsterdam, the suture of Text-figure 2F was taken from the specimen illustrated here on figures 15, 16.

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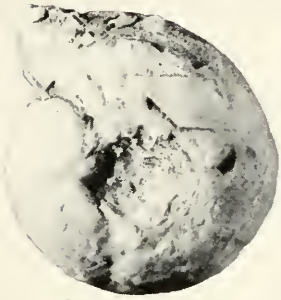
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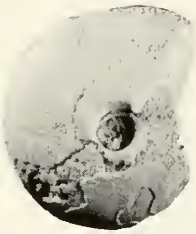
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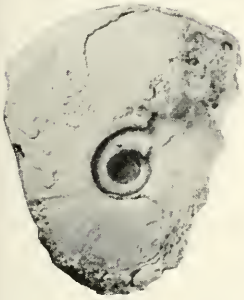
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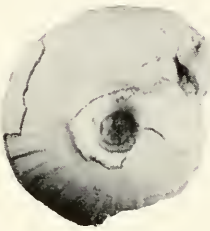
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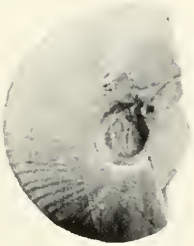
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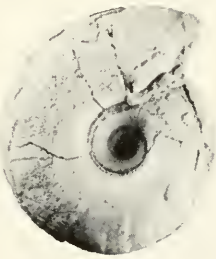
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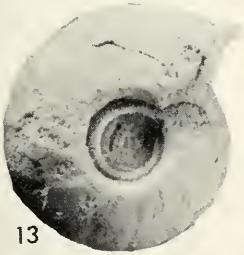
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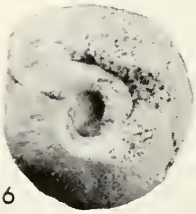
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THE RELATIONSHIPS OF *ANOLIS* OF THE *ROQUET* SPECIES GROUP (SAURIA:IGUANIDAE) — III. COMPARATIVE STUDY OF DISPLAY BEHAVIOR

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INTRODUCTION

In separate papers on chromosome cytology and electrophoresis of blood proteins (Gorman and Dessauer, 1966; Gorman and Atkins, 1967), the relationships of the *roquet* group of *Anolis* have been discussed in detail. The present paper is an attempt to use comparative ethology as an additional index of relationship and evolutionary history of the group. No attempt is made here to provide an "ethogram" of any of the forms. Instead, some stereotyped action patterns that vary from island population to island population are compared as taxonomic characters.

Taxonomy and Distribution

Eight forms are considered in this paper. The species of the *roquet* group are found on all the islands of the Lesser Antilles from Martinique south to Grenada and west to Bonaire. To the north of Martinique are anoles of the *bimaculatus* group; to the south, on Trinidad (a continental island), and to the west, on Curacao and Aruba, are members of the *chrysolepis* group (classification into species groups follows Etheridge, 1960). These species groups seem to exclude each other, and the only recorded overlaps (on Trinidad, St. Lucia, and Guayana) appear to be recent introductions (Gorman and Dessauer, 1965, 1966). Figure 1 summarizes the distribution of the group.

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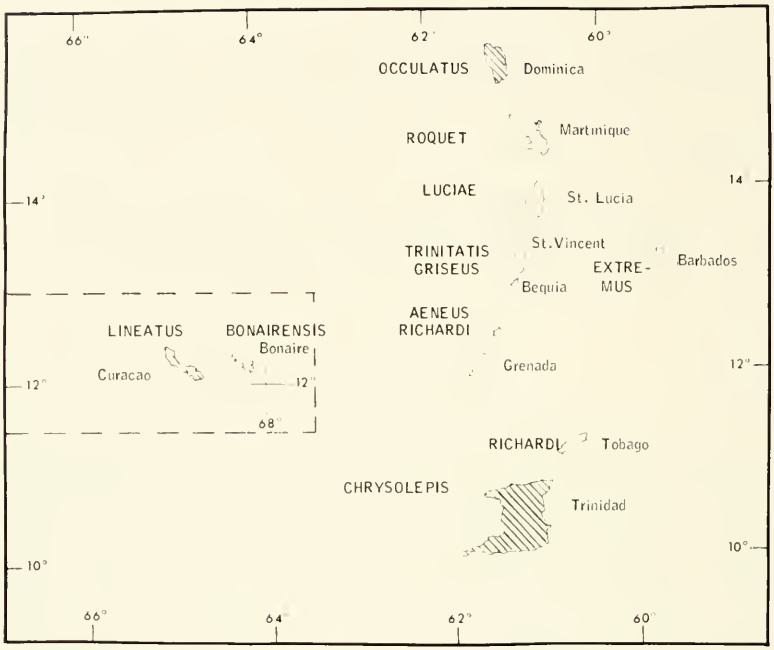

Figure 1. The distribution of *Anolis* of the *roquet* species group (unhatched islands). Names of forms considered, in capitals. Names of islands, in capital and small letters. The anoles on the islands indicated by oblique lines are not in the *roquet* group.

By the use of chromosomes and blood proteins, the species group has been divided into several subgroups and species designated. A basic dichotomy exists in chromosome number. Three forms have 2n=34, the other five have 2n=36. The latter is the presumably primitive number for the family Iguanidae (Gorman, Atkins, and Holzinger, 1967).

Those anoles with reduced diploid number have always been considered very closely related on morphological evidence. Reduction in chromosome number is rare and generally an advanced character, and this is taken as additional evidence that indeed these three anoles form a natural subgrouping. For reasons documented elsewhere (Gorman and Dessauer, 1966), similarity in

hemoglobins was used to define species. Thus the group could be divided in the following manner:

2n = 36 { *luciae* / *trinitatis* / *bonairensis* / *richardi richardi* / *richardi griseus* } common Hb

2n = 34 { *roquet roquet* / *roquet extremus* / *aeneus* } common Hb

In the 2n=36 group (primitive) *A. r. richardi* and *A. r. griseus* form a natural subunit characterized not only by proteins but by giant size.

An hypothesis about the biogeographic movements of the group is being presented in a separate paper (Gorman and Atkins, 1968). The defense of this hypothesis will not be repeated here. However, it is presented as a working model with which the behavorial results may be compared.

A. luciae is considered the most primitive member of the group. Reasons include chromosome number, size (intermediate between the giants and the other five forms), and geographic position (more or less in the center of the group.) From St. Lucia, St. Vincent was twice colonized, leading to two species, *trinitatis* (small) and *griseus* (giant). From St. Vincent, the two reached Grenada and through further differentiation have become *aeneus* (small) and *richardi* (giant). *A. richardi* has reached Tobago without further differentiation. The small Grenada species colonized Barbados *(extremus)* and from there Martinique *(roquet)*. Or, alternatively, the small St. Vincent form *(trinitatis)* colonized Barbados directly, followed by a double radiation from Barbados to Grenada and Martinique.

Behavior in *Anolis*

Because of the elaborate displays of these strongly territorial lizards, the *Anolis* species have been of long-standing ethological interest. Greenberg and Noble (1944) presented the most comprehensive discussion of a single species, *A. carolinensis*. This report was based upon four years of observation of approximately 600 lizards. Included in their paper are sections on aggression, courtship and mating, egg laying, dominance, subordination and hierarchies, territory, and sex recognition. Other studies, such as Kästle's (1963) on *Norops (= Anolis) auratus*, Carpenter's (1965) on *A. townsendi*, and Evans' (1938) on *A. sagrei*, provide valuable descriptions of displays and social behavior in single species.

The only attempt at a broad comparative survey of *Anolis* behavior was by Ruibal (1967), who described aggressive displays in twelve species of Greater Antillean *Anolis*.

The genus is divided into two major groups (alpha and beta), based on an osteological difference (Etheridge, 1960), and supported independently by chromosome differences (Gorman, 1965). Ruibal (1967) was interested in determining if there was any parallel between the alpha-beta dichotomy and behavior. Although Ruibal found species-specific differences, he wrote, "the analysis of the initial response in these anoles demonstrates that the behavioral patterns are of limited value in determining relationships within the West Indian species of *Anolis*."

My own study, presented here, indicates the value of behavior as a systematic character *within* at least one species group.

METHODS

In 1963-64, I spent 10 months in the Caribbean area, based at the University of the West Indies in Trinidad. Subsequently, several additional brief visits were made to the islands where the *roquet* group occurs, as well as to neighboring islands. At first, the lizards were simply observed in the field and extensive notes on ecology and behavior were prepared. Later, they were studied in cages at the University of the West Indies. In general, two adult males were placed on opposite sides of an opaque partitioned cage. Several hours to days later, the partition would be removed and social interactions described. To gather quantifiable data the lizards were photographed on 16 mm motion picture film. The bulk of the data presented are from analysis of films made in the field. In some cases the films are of natural interaction, but high intensity territorial disputes are not frequent in natural situations; they are easily elicited, however, by tethering an "intruder" to a long pole and placing him within the territory of a resident. Films were analyzed on a Weinberg-Watson single frame analyst. This allows frame-by-frame analysis of the temporal sequence of displays. Amplitudes of movements were not measured precisely but were estimated. No great emphasis has been placed upon amplitude differences in display.

Elicitation of Display

Iguanids respond to visual cues. The introduction of a mirror into a cage elicited highly stereotyped displays identical to those

seen in the field in natural encounters. Carpenter (1962) has reported results of mirror experiments in *Sceloporus,* and a rather accurate description of an *A. roquet extremus* display to a mirror was written for a popular audience by Dr. Maurice Burton (London Illustrated News, 29 August 1964).

Neither the opponent's dewlap color nor the dewlap *per se* seems to be of great importance in eliciting a response from a resident. Greenberg and Noble (1944) found that restraining the dewlap by means of a collodian coating did not affect the social status of the male. Dominant animals were still able to hold territory and win combats with normal rivals. In addition, normal males displayed to males unable to extend the dewlap.

I have found that members of the *roquet* group in captivity will display to other species if these are in the same size range.

A planned experiment to study releasers by use of models presented to residents in the field was thwarted at the outset. *A. trinitatis* are very abundant and quite willing to display to other anoles in the Botanic Garden in St. Vincent. A life-size wooden model of a male *trinitatis* was constructed and, I thought, accurately painted. A slit was made in the throat region for insertion of paper dewlaps of the "right" or "wrong" color. If males responded aggressively to the model, then variations in size and color were planned to elucidate exactly which parameters were important to a resident territorial male. However, responses to the dummy were uniformly negative.

Experiments involving a decapitated intruder were somewhat more successful. The decapitated head was pinned to a piece of sponge, cut approximately in the shape of a lizard torso. Several resident males attacked and/or displayed actively to this model, and even to the decapitated head alone, when dangled freely. This experiment was terminated when a *griseus* ran down from the crown of a tree and grabbed and ate the *trinitatis* head.

In a reciprocal trial, a head-sized piece of sponge was pinned to the body of the decapitated lizard. This did not elicit aggressive display. Some males were painted bright red, others bright white. Results in several trials were equivocal. Some residents displayed or attacked, others fled from the intruder. Thus, something in the configuration of the head probably acts as a releaser.

Another apparently important component in elicitation of display is movement on the part of the intruder. A tethered male will usually flatten himself on the substratum in a classically submissive

posture.[1] The resident will watch. Slight jiggling of the intruder is sufficient to elicit immediately a high intensity response (biting attack or display).

Description of Display

Carpenter (1962) has standardized his descriptions of iguanid behavior by describing eight characteristics of display — site, position, posture, movement type, parts moved, units of movement, sequence, and cadence.

Ruibal listed and defined the following movements and postures to describe aggressive encounters in *Anolis*.

1. Dewlapping — the characteristic erection of the large gular appendage.
2. Bobbing — the vertical motion of the head.
3. Pushups — an extension of the limbs to raise the body off the ground.
4. Tail wags — vertical or horizontal movement of the tail.
5. Tail lashes — a very exaggerated movement of the tail in a broad whipping manner.
6. Tongue — the tongue may be everted and protruded from the mouth and in some species may become purple with engorged blood.
7. Nuchal and dorsal crests — the dorsal regional of the neck and the middorsal region of the body are usually raised as thin fins.

Application of these descriptions to the *roquet* species group would be as follows:

A. The eight categories of Carpenter.

1. Site: All the anoles of the *roquet* group are strongly arboreal. Most daytime observations are made of animals on tree trunks four to seven feet above the ground. Most displays are given when the lizards are on tree trunks; however, during a battle they will display from the ground. When they display they try to find a slightly elevated site, such as a knot on a tree.

2. Position: Orientation is usually perpendicular to the recipient of the display. If the opponents are parallel, then the heads are facing each other. The position chosen maximizes the opponent's view.

[1] Darwin (1872) pointed out that submissive postures were often the antitheses of aggressive ones. Thus, in the anoles in submissive posture the crests are down, dewlap in, body low.

3. Posture: In aggressive encounters, nuchal and dorsal crests are generally raised. As noted by Greenberg and Noble (1944) for *A. carolinensis*, "The initial hostile reaction is a puffing or gorging of the throat followed almost immediately by lateral flattening so that the male appears much larger from side view." This serves as an excellent description for the *roquet* group and shall be referred to as "engorged head."

These three categories are not of further use in this comparative study because they are constant for the species group.

4-6. Movement type, parts moved, and units of movement are encompassed by Ruibal's categories, and are discussed below.

7. Sequence: The order of appearance of units of movement will be exemplified by quotations from notes on actual encounters.

These categories again are consistent for the species group.

8. The measured time for the performance of each unit of movement. This is *the* important category employed in comparing displays within the species group.

B. The seven movements of Ruibal.

1. Dewlapping: The dewlap of the *roquet* group and all its near neighbors is well developed. The cadence of extension differs between the *roquet* group and the anoles that geographically surround it.

2. Bobbing: In the *roquet* group all eight forms bob the head in high intensity display, and each form shows a temporal sequence that is unique. I also refer to nodding, in which the head is raised and lowered very slowly. This is a less stereotyped movement and seems to occur at lower intensity.

3. Pushups: Again, all forms in the group rise up on all limbs in high intensity display. Some have also been observed to include "rhythmic movements" as a part of the challenge display. This is a series of movements at very precise intervals — it may simply be head bobs, or pushups, or pulsating locomotion.

4. Tail wags: Horizontal movement of the tail is seen under situations of stress. It occurs when two anoles are actually fighting and is not seen in the clearly dominant animal. It also occurs when an anole is captured by a herpetologist and is held in the hand.

5. Tail lashes: All species of the *roquet* group may use the tail in a challenge display. The frequency and amplitude of tail lashes is an important character in tracing relationships.

6. Tongue: Several members of the roquet *group* have been seen to protrude the tongue during display. I do not know how frequent or how widespread this movement is. The tongue is

engorged with blood and quite bright in color. At the termination of the display, while the dewlap is being retracted, the mouth is opened and closed several times as though a swallowing movement were occurring. This has been recorded for *A. r. roquet, A. trinitatis* and *A. bonairensis* and may be present in the other species.

7. Nuchal and dorsal crests: Present and raised in all species during aggressive encounters.

THE DISPLAY CATEGORIES OF THE *ROQUET* GROUP OF *ANOLIS*

There are three obvious categories of display in this species group: activity bobs, courtship, and aggressive display. Only the last was studied in detail.

(1) The activity bob corresponds to Carpenter's (1962) "Assertion Display." For example, in changing position a lizard may run a few feet, stop, bob, run a few more feet, stop, bob, etc. This bob is also commonly seen after feeding. I have reason to believe that it is stereotyped and may be species-specific. However, I do not have enough data to discuss it further. This bob is most commonly given by females.

(2) Courtship was difficult to study under field conditions, as most displays directed by males to females were followed by rapid departure by the female. There are no obvious differences among the species in courtship display, and my observations are concordant with those of Greenberg and Noble (1944) on the following points:

a) There is no sign of aggression; *i.e.*, engorged head, crest erection, and tail jerks are all absent.

b) The approach pattern differs from the aggressive encounter in that there are numerous rapid low amplitude bobs and an irregular, jerking walk.

(3) Aggressive display.

The most elaborate of the displays are also the most stereotyped, hence the most useful for analysis of evolutionary relationships. Intensity of display obviously varies, as has been pointed out by Kästle (1963) and Ruibal (1967). Ruibal limited his study to what he called the "initial response," which he defined as "the immediate and first response of the test animal to the decoy." Later he states that it is comparable but not identical to the challenge display of Carpenter (1962) — "the initial response actually represents the first part of the challenge display."

I agree completely with Ruibal that there is a predictable, stereotyped portion of lizard display behavior. However, the term "initial" in Ruibal's phraseology is unfortunate, because the literally immediate response of a resident male to an intruder is quite unpredictable: the resident may flee, go into the engorged head posture and wait, attack by biting, or display at varying intensities. I prefer to use the term challenge display.

All eight members of the *roquet* group have challenge displays which follow a definite sequence of actions: (1) extend dewlap; (2) rise high on all four limbs; (3) raise the tail, then lower it; (4) lower the body; (5) give rapid head bob; (6) retract dewlap.

The following excerpt from my field notes will exemplify this pattern:

A. r. roquet — Martinique — 2 July 1965:

> A tethered male intruder is placed about 12 inches above a resident male (R) perched on a tree. The intruder starts running away from resident. R slowly moves up several inches, pauses. Intruder jiggled. R backs away. R turns perpendicular to intruder. Intruder moves and R follows, stopping a foot above. Head is in engorged position R moves to two feet above intruder; extends dewlap fully; rises high on all four limbs; 5 tail lashes; lowers body; dewlap half retracted. R pauses for several seconds. Extends dewlap fully while body rising high on all four limbs. Tail raised high and then lowered slowly. Bobs head. Retracts dewlap. Display is repeated again.

Note that the sequence of movements is the same in the two full displays, but in the first instance head bobbing did not follow the tail movement.

The six sequential steps of the challenge display are present or absent in independent fashion, but when they do appear they are evidently never out of order. That is, the dewlap might not be extended but the resident male still lashes his tail and then bobs; or he may omit the bobs, or he may not fully retract the dewlap at the end of the sequence. However, he will never bob, then lash the tail, and then extend the dewlap.

Some of the steps are better correlated than others. The tail movement almost always occurs with the dewlap fully extended. And, if there be a rapid bob with dewlap extended, the dewlap is almost always retracted at the end of the sequence unless the displaying lizard immediately launches into a new sequence.

The high intensity challenge display is interpreted as occurring when there is an intermingling of attack and withdrawal stimuli. The elaborate display is often preceded by backing away from the intruder. Indeed, the displays often follow unsuccessful direct

attacks. The following encounters may serve as illustrations.

1. *A. trinitatis* — St. Vincent — 8 July 1966:

Intruder is placed three feet below resident who is 10 feet up in a coconut tree. R runs down, bites at intruder. Bites again. They lock jaws. R breaks away and runs back up. Bobs rapidly. Attacks again several times, biting at the head of intruder. R backs away. Extends dewlap half-way. Rapid bob. R attacks again. Grab jaws. R flipped to ground.

2. *A. r. roquet* — Martinique — 3 July 1965:

Tethered male intruder placed four feet below resident who turns immediately, runs down and stops one foot above intruder. Pauses. Then rushes at intruder and bites at head; extends dewlap, bobs. Runs jerkily above intruder; full dewlap extension, head bob, dewlap slowly retracted. This is repeated again. Then R moves toward intruder and bites at him. R then backs away and moves to one foot above intruder. Dewlap fully extended, head bobs, then dewlap retracted. Repeated several times. Each time there is a slight movement of the intruder, there has been a full dewlap extension followed by head bobbing. Resident then runs to one foot above intruder. Faces down and is approximately perpendicular. Rises high on all four limbs, tail comes up slowly; full dewlap extension; body lowered, head bob, dewlap retracted. Then R moves up and away from intruder.

In Trinidad, I filmed a long sequence of a male *A. aeneus* displaying to a tethered intruder in which the resident gave the full display, then ran up and away from the intruder. I then moved the intruder up a comparable distance, the resident again quickly displayed and moved away again. This was repeated several more times.

These examples serve to support the hypothesis that the elaborate challenge display is not simply a ritualization to avoid physical fighting, but rather a display given in a situation with conflicting stimuli of attack and flee. Under natural field conditions these displays have been seen only when the opponents were extremely evenly matched. Usually the engorged head of a dominant resident is enough to stimulate flight in a subordinate or intruding male.

Combat is by no means always the initial high intensity response, as the following notes indicate.

A. r. roquet — Martinique — 3 July 1965:

Intruder placed near male resident who immediately goes into engorged head posture and moves down toward intruder. R extends dewlap fully and rises up on all four limbs; three tail lashes; dewlap slowly retracted.

Some encounters are settled without actual biting. I once witnessed a very lengthy dispute between two male *A. trinitatis* in

the Botanic Gardens of St. Vincent. Both were on a broad tree. At the start, one was about two feet above the other. After some fifteen minutes with dozens of high intensity displays, they slowly moved towards one another and, when contact was made, they butted heads, snouts pointing downwards. Then one backed off and climbed up and around the tree.

Although all these encounters describe males, females also display to females. Although the secondary sexual characters of dewlap and crests are much reduced, and the females are also much smaller than adult males, the postures and motions appear identical to those of males. I never saw a natural interaction between females, but did observe and film female display by use of a tethered intruder.

SYSTEMATIC SECTION

I. Definition of the *roquet* species group on the basis of behavior

Although each of the eight forms has a display which is quite distinct because of variation in cadence, all members of the species group have basically a very similar display. In the use of the dewlap, the *roquet* group differs from its near neighbors in the *chrysolepis* and *bimaculatus* groups. Thus, behavior provides further evidence that the group is a natural evolutionary unit.

In all eight forms, the dewlap is extended and held out for the entire display sequence, and sometimes is not retracted at the end of the sequence. The dewlap is never pumped in and out in any rhythmic manner. This contrasts sharply with the other Lesser Antillean anoles. Figure 2 illustrates the challenge display of *A. roquet extremus*.

In place of the activity bob, members of the *bimaculatus* group seem to have a true assertion display *sensu* Carpenter. I have watched and filmed *A. oculatus* on Dominica pumping the dewlap in and out in a slow rhythmic manner — even when no recipient of the display was apparently present. In high intensity challenge, dewlap pumping is an integral part of a complex display which also involves bobbing and tail movements.

A. lineatus (*chrysolepis* series of beta anoles) of Curacao also pumps the dewlap. This species is quite unrelated to the *bimaculatus* group (alpha anoles), and serves to illustrate the problem Ruibal (1967) encountered in a search for a major diagnostic character to split the genus by means of behavior.

Figure 2. Challenge display of *A. roquet extremus*. Dewlap fully extended, tail up, and body high off the perch.

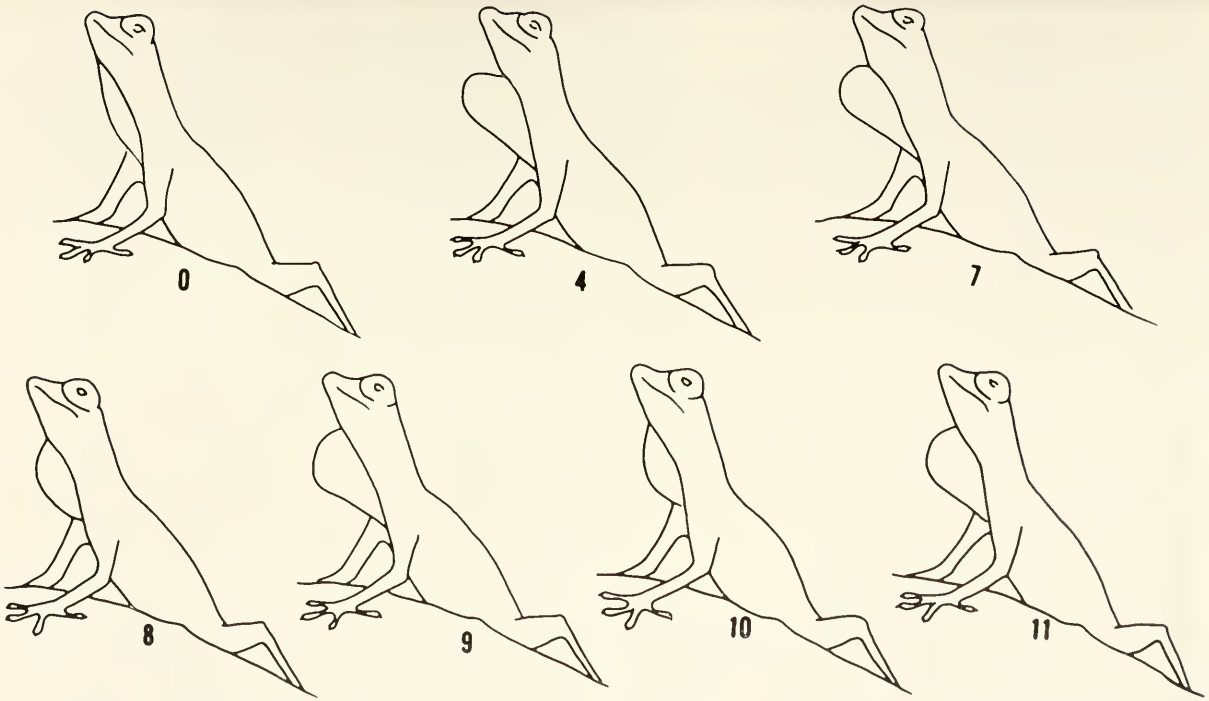

Figure 3. The challenge display of *A. chrysolepis*. This consists of rapid flashes of the dewlap while the body is in a stationary position. The drawings are from a display filmed at 16 frames per second.

The number under each drawing corresponds to the number of frames (time elapsed in units of sixteenths of a second from starting time 0).

A. chrysolepis of Trinidad and the South American mainland displays by flashing the dewlap extremely rapidly and in a stereotyped manner. The entire display appears to consist of dewlapping. The head is held high but is not bobbed. Figure 3 shows *chrysolepis* in challenge positions.

Because dewlapping is widespread in both the alpha and beta anoles, it is interpreted as a primitive character which has been secondarily lost in the *roquet* group. Further evidence for this will be presented below.

II. Description of the challenge display of *A. luciae*

A. luciae is considered the most primitive member of the species group. It is thus worth analyzing its display in some detail, to serve as a basis for comparison.

Descriptions of interactions

1. Forestiere, St. Lucia — 6 July 1965

Resident male is high in a tree. Tethered intruder placed four feet below him. R rises up on all limbs, extends dewlap, tail goes up once, then down. Bobs head. There are four distinct series of bobs while the dewlap is held out. Dewlap slowly retracted.

2. Vigie Beach, St. Lucia — 6 July 1965

Resident male is in a breadfruit tree. Intruder placed one foot below him. R immediately orients perpendicularly to intruder, head facing head. Resident rises up high. Extends dewlap and bobs head. The head bobs are in four distinct series, with a partial dewlap retraction following each series. Intruder turns, and R turns, maintaining perpendicular orientation. Repeats display, again with four series on a single dewlap.

The display of *luciae* may be characteriezd as distinct from other members of the *roquet* group by the following:

1) Tail — the tail is infrequently used in display sequence. When it is used, it is raised once slowly, then lowered.

2) Head bobs — *luciae* has a head bob sequence that is extremely long in duration and that is clearly divided into several series. That is, a series of bobs is followed by a pause, followed by a series of bobs, followed by a pause, etc. (Figs. 4L and 5L).

3) Partial dewlap retraction — during the long pauses, the dewlap is very slightly retracted, then re-extended. *A. luciae* is the only member of this species group to move the dewlap at all

in mid-sequence. This movement might be a vestige of the dewlap pumping common to most *Anolis*.

The following quantitative data were analyzed:

1) Number of peaks preceding a pause. A pause was arbitrarily defined as 6/16 of a second (N.B. all films were made at 16 frames/second, and time units discussed are in 16th of a second or frame) with no head movement. A peak was defined as the highest point the head reached before the next downward movement. Thus sub-peaks were not counted. The distribution in number of peaks per bobbing series proved to be quite variable, with a range from 1-18. However, the mean is 5.2 and 54 per cent of the sequences had 4, 5 or 6 peaks.

2) The time interval of bobbing series was also measured. Again the range is very broad, 2-47 frames. The mean is 18.

3) The pause lengths between bobbing series were also measured and the distribution of these time intervals is shown in Figure 7. Note that the first category is also the largest. This is probably an artifact — *i.e.* a pause was defined as 6 or more frames. This does not mean that it is necessarily a "real" pause to the animal. If 10 or more frames were chosen as the arbitrary limit, there would be a gradual rise in frequency to the 30-33 frame class, and then a drop. No relationship could be demonstrated between the number of peaks in a sequence and the length of the following pause.

Two other categories also easily lent themselves to quantitative analysis: number of bobbing series in a single display sequence, and total time elapsed in the full bobbing sequence. Because of the repetitious nature of the long displays and the high cost of motion picture film, few full sequences were filmed. Some examples are tabulated below:

No. bobbing series	Total time	Full sequence filmed
5	10.5 sec.	no
3	8.5	yes
5	19.3	yes
5	12.5	yes
4	12.5	no
3	6.7	yes

The total elapsed time for a full bobbing sequence in *A. luciae* is far greater than for any other member of the species group.

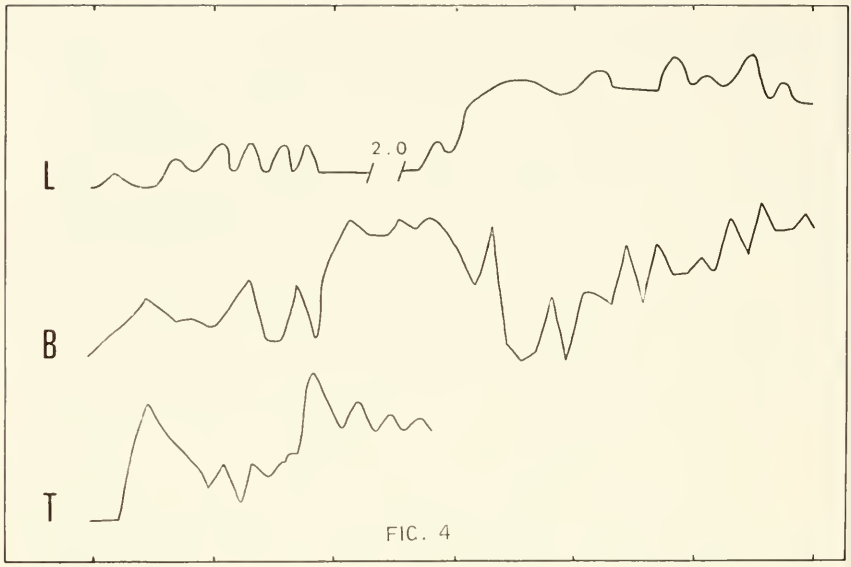

FIG. 4

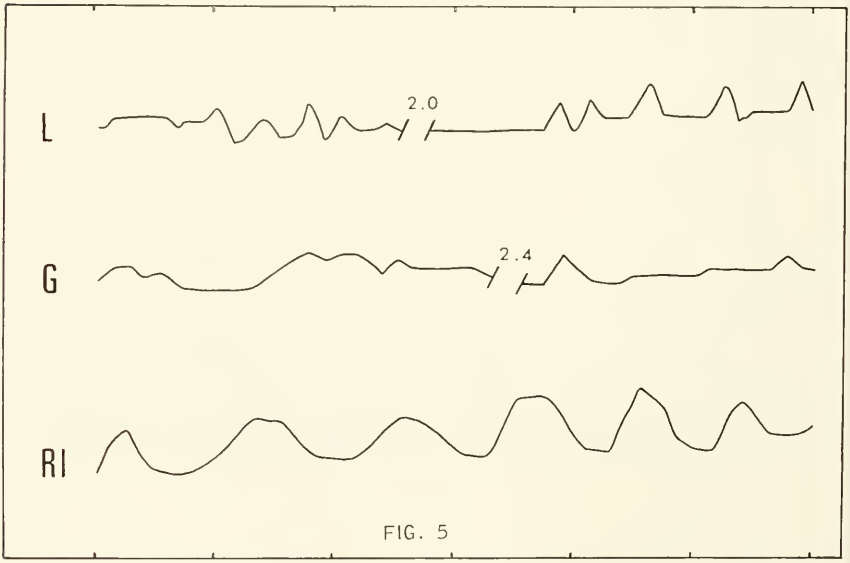

FIG. 5

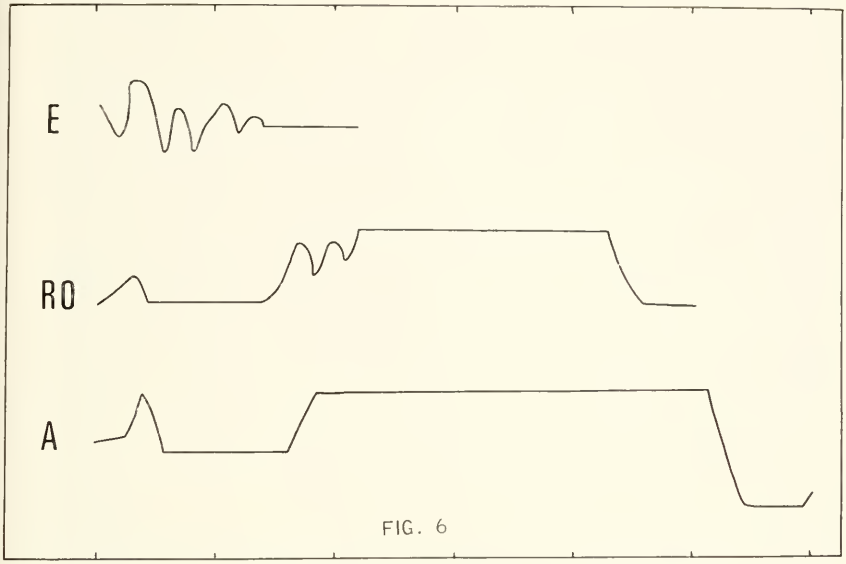

FIG. 6

Figures 4-6. Head bobbing sequences in *roquet* group *Anolis*. Time intervals are one-half second between successive dots on upper and lower borders of each figure. Long pauses are indicated by a break, with the time interval in seconds written in.

Figure 4

L. *A. luciae*
B. *A. bonairensis*
T. *A. trinitatis*

Figure 5

L. *A. luciae*
G. *A. richardi griseus*
RI. *A. r. richardi*

Figure 6

E. *A. roquet extremus*
RO. *A. r. roquet*
A. *A. aeneus*

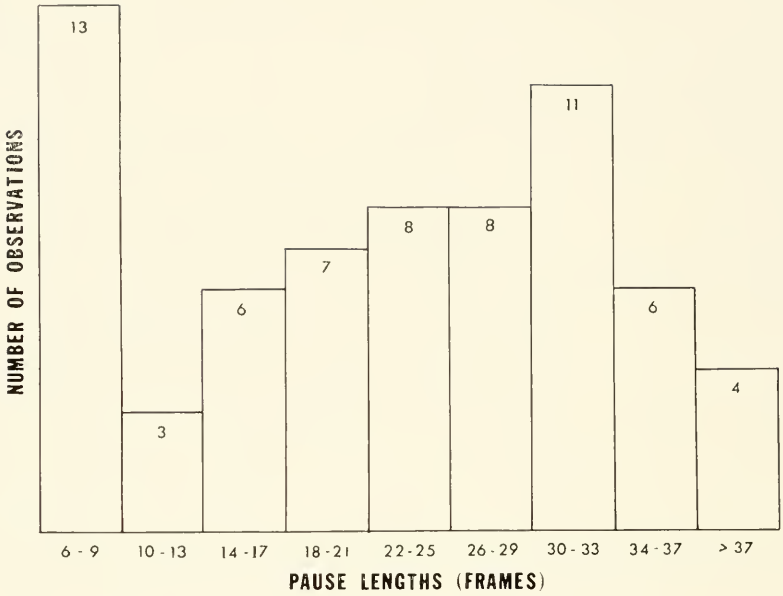

Figure 7. The frequency distribution of pause lengths which precede subsequent bobbing series in *A. luciae*. One frame is equivalent to one-sixteenth of a second.

III. Presumed derivatives of *A. luciae*

A. luciae, for reasons stated earlier, is presumed to be the primitive member of the species group. Following the model presented in the zoogeographic study of the *roquet* group, three forms are believed to be derived directly from *luciae:* double colonization of St. Vincent from St. Lucia gave rise to *trinitatis* and *griseus*, and colonization of Bonaire gave rise to *bonairensis*. In this section we shall compare the displays of these three forms to those of *A. luciae*.

a) *A. bonairensis*.

The relationships of this species to the remainder of the species group are probably the least clear. Bonaire is far west of the Lesser Antillean chain (see Figure 1), but the anoles on the adjacent islands just west of Bonaire are certainly unrelated to *bonairensis*. When the species was described (Ruthven, 1923), it was compared with *roquet* and *aeneus*. The osteological study of Etheridge placed this form very close to the other members of the

roquet group, and this was confirmed by blood proteins and chromosomes. In our paper on blood proteins (Gorman and Dessauer, 1966), it was pointed out that although *bonairensis* was clearly a member of the *roquet* group, it was not particularly close to any one form. We speculated that it might be derived from *aeneus*, since Bonaire is due west of Grenada and the general current flow is westerly.

However, when we examined chromosomes (Gorman and Atkins, 1967), we found that *bonairensis* belonged to the more primitive group (2n=36), making it highly improbable that it was derived from *aeneus*. The geographically intermediate form *A. bonairensis blanquillanus* has been unavailable for study.

It is, of course, possible that Bonaire was colonized independently by a mainland South American *Anolis*. However, that is not likely. Although the *roquet* group forms are clearly allied to South American alpha anoles, they share a unique complex of osteological and biochemical characters which most likely evolved in the Lesser Antilles.

Thus our hypothetical ancestor would be a *luciae*-like or *trinitatis*-like anole. J. D. Lazell, Jr., who is studying the external morphology of Lesser Antillean anoles, relates *bonairensis* to *luciae* (personal communication).

The display of *bonairensis* is basically similar to other members of the species group. It may include tail lashes and head bobs.

Description of an interaction

4 May 1964

Intruder placed on a tree. Resident male comes running across a fallen stump to stop 2 feet from intruder. He runs at least 15 feet. Head is in engorged posture. I jiggled intruder, R immediately extends dewlap fully, rises high on all four limbs, tail is raised once, dropped, body lowered. Bobs head and retracts dewlap.

The head bob sequence of *bonairensis* is unique in the large number of peaks and the great length of time. The bobbing may or may not be broken up by pauses of 6 frames or longer. In 20 filmed sequences, 14 are without pauses. These sequences have a range of 12-23 peaks (mean 17.7) and a time range of 43-95 frames (mean 62.2). Of six sequences with pauses, five have only a single pause and one sequence has two pauses. This last case may be an artifact, for the first pause follows a single slow head rise, which is probably not part of the bobbing sequence. As opposed to *luciae*, which has pause lengths of as long as 40+ frames, the

pauses of *bonairensis* are all short, ranging from 6-10 (mean 8.3) frames.

Those sequences which have pauses range in total peak number from 13-24 (mean 17.7), which is almost identical to the non-pause displays. The total time intervals range from 47-91 frames (mean 69.0), which is within the range of non-pause displays.

Thus the head bobbing sequence of *A. bonairensis* is best described as a long single sequence with many peaks, occasionally broken into two series. The display of *bonairensis* could be derived from the *luciae* display with but one minor alteration: elimination of the pauses which break the bobbing sequence into distinct series.

Bonairensis also uses tail lashing in high intensity displays. In this respect the species resembles other members of the *roquet* group more than *luciae*.

b) *A. trinitatis*.

A. trinitatis is the widespread small anole on St. Vincent. It also occurs on Trinidad, where it was probably introduced by man. On Trinidad it hybridizes with *aeneus*. A detailed analysis of hybridization is being prepared. The data on *trinitatis* presented in this paper include St. Vincent and Trinidad specimens, as no discernible difference could be found in their displays.

The challenge display of *trinitatis* consists of very rapid tail lashes followed by rapid bobs. Long pauses are infrequent. A slow tail movement has not been observed. Figure 8 compares the characteristic rapid tail movement of *trinitatis* with that of *extremus*, which is slow. Descriptions of encounters appeared in the introductory part of this paper.

The variation in 30 rapid bob sequences of *trinitatis* is:

Rapid bob time interval		No. peaks per bobbing sequence
range (sixteenths of a sec.)	12-31	2-10
mean	23.0	5.7
		56% are 4, 5, or 6

A typical rapid head bob of *trinitatis* is presented in Figure 4T.

The full bobbing sequence in *trinitatis* resembles a single series of bobs within a sequence in *A. luciae*. The display of *trinitatis* differs from that of *luciae* in the rapid tail lash and in the shorter, non-paused head-bob sequence. The latter, however, could easily be derived from a foreshortening of the *luciae* display.

c) *A. richardi griseus*.

Although this is the largest, it is paradoxically the shyest member of the *roquet* species group; that is, *A. r. griseus* is quick to

flee at one's approach. As a result, I have few data. No natural aggressive interactions were seen. Two males did display to tethered intruders, and their several bobbing sequences were recorded on film. These two males were filmed in the summers of 1964 and 1966, respectively, and on opposite ends of St. Vincent. The display action patterns are quite similar. Thus, although lacking details on the total range of variation display, the data are probably valid from the broadly comparative viewpoint.

High intensity display consists of dewlap extension, rapid tail lashes, head bobs, and dewlap retraction.

The head bobs are in series, as in *A. luciae*. Figure 5G illustrates a typical bobbing sequence of *griseus*.

I do not have enough pauses measured to compare in detail, but here too the distribution seems similar to *luciae*. Of 11 measured pauses, 5 are between 6-9 frames, 5 are 20 or more frames, and only one falls between these two intervals (compare with Figure 7).

There does seem to be a reduced number of peaks per series; in 18 measured series the mean is 3.3, and 61 per cent of the sequences have 1, 2, or 3 peaks. In *luciae* the mean is 5.2, and 54 per cent of the series have 4, 5, or 6 peaks. However, the mean time interval per bobbing series (16.6 frames) is very close to that of *luciae* (18.0). This implies that the head bobs of *griseus* are broader (slower) than those of *luciae*. Such a trend can be seen by comparing Figures 5L and 5G.

The total time of a bobbing sequence, adding all series and pauses, may also be shorter than in *luciae*. (Compare these data with those on p. 15.)

No. bobbing series	Total time	Full sequence filmed
2	5.0 sec.	yes
2	4.8	yes
5	8.4	yes
4	7.3	yes

In summary, the displays of *griseus* are quite similar to those of *luciae*. In head bobbing there seems to be a tendency for fewer peaks per series without a significant decrease in the time of the series, whereas the total time of a bobbing sequence is reduced.

Also, *griseus* may use several vigorous tail lashes in the challenge display, whereas *luciae* does not use the tail frequently, and does not use multiple lashes when it does use the tail.

IV. Presumed derivatives of *griseus* and *trinitatis*

a) *A. r. richardi.*

A. r. richardi is very closely related to *griseus*. On the basis of blood proteins (Gorman and Dessauer, 1966), the two forms were considered conspecific and distinct from all other members of the species group.

Unlike *griseus*, *richardi* is not shy, and numerous displays have been observed in Grenada and in Bequia, the northernmost of the Grenadines. No displays were studied in Tobago.

Descriptions of encounters

1. St. George's, Grenada - 17 July 1965

A male resident is seven feet up in a mango tree. Intruder placed two feet below. R immediately into engorged head posture watching intruder. Intruder runs up. R extends dewlap fully, rises up high on all limbs, tail up a bit, then down slowly. Again up and then down slowly, dewlap still out. Intruder removed.

This is interpreted as a low intensity response. Male *richardi* may rise up slowly and the head is sometimes slowly nodded. The following is an example of a high intensity response, the type of response that was analyzed.

2. Beausejour, Grenada - 17 July 1965

Intruder placed near resident male. Dewlap extended. No tail motion. Bobs vigorously about 7 times. Dewlap partially retracted. Intruder jiggled. R rises up, lashes tail four times, then a fifth time with lower amplitude. Dewlap is held out. R looking at intruder. Intruder removed.

The high intensity display of *richardi* is characterized by vigorous tail lashing, followed by head bobbing.

Unlike *griseus*, there are not multiple series, but rather a single series, in a bobbing sequence. Figure 5 RI shows an example of *richardi* head bobs. These bobs are broad, *i.e.* the rise and fall are relatively slow and the peak is flatter than in *griseus*. The display appears much more stereotyped than that of either *luciae* or *griseus*, both in number of peaks (range 4-7, mean 5.8) and in total elapsed time in the bobbing sequence (range 39-58, mean 47.3 frames). Although there are only eight filmed displays, numerous other displays observed in the field seemed to conform to these ranges.

b) *A. aeneus, extremus* and *roquet.*

These three forms are very closely related and were considered conspecific by Underwood (1959), although he later changed his mind (1962). They were first studied biochemically by Gorman

and Dessauer (1965), who found that on the basis of electrophoresis of serum proteins they were closely related, and a linear chain of relationship could be established: *aeneus* and *extremus* differ in hemoglobin mobility, *extremus* and *roquet* in transferrin mobility, and *aeneus* and *roquet* differ in both these characters. In a more detailed study of blood proteins encompassing the entire species group (Gorman and Dessauer, 1966), *extremus* was recognized as a subspecies of *roquet*, and *aeneus* was recognized as a

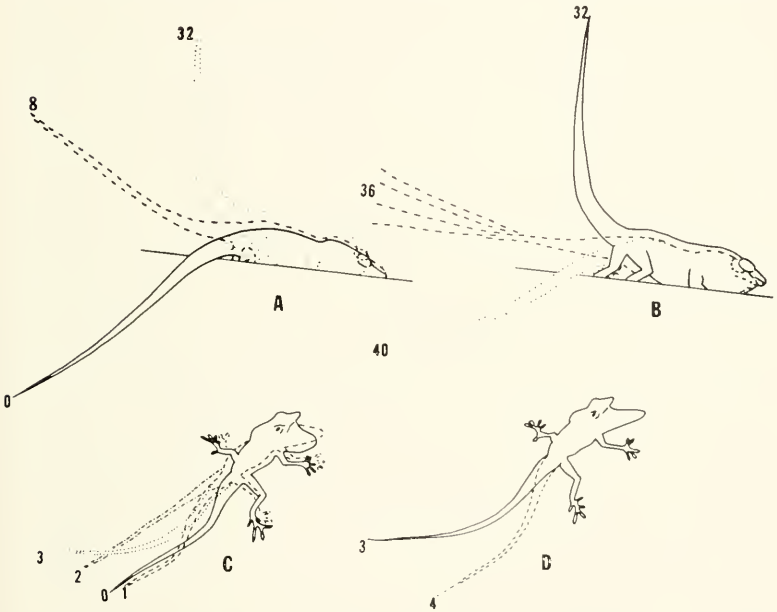

Figure 8. Comparison of the slow tail movement of *A. roquet extremus* (upper) with the rapid tail movement of *A. trinitatis* (lower). Numbers at the tip of the tail indicate frames elapsed from start of display (one frame equal to 1/16 second).

A. Tail rise in *extremus*. The tail is slowly arched up. A full two seconds elapse before peak is reached.

B. Tail lowering (same display). The tail is dropped more quickly than raised. Multiple dashes at 36 indicate tail was in rapid motion and film was blurred on that frame. Total time interval for sequence is 40 frames (2½ seconds).

C. Tail rise in *trinitatis*. The peak is reached in 3 frames.

D. Tail lowering (same display). The tail is down one frame later. Total time interval, 4 frames (¼ second). The drawings were made by superimposing images from a single frame projector.

species. The three forms are obviously very close to *trinitatis*. The chromosome study showed that *trinitatis* was a likely ancestral form, as it had the primitive chromosome number.

In display behavior, there are great similarities among the three in gross movements. That is, the sequences of movements are identical, all have a variable tail movement, slow to moderately fast — but always slower than *trinitatis* (Figure 8) — and all bob the head. But here there are consistent differences.

A. r. extremus has a head bobbing pattern that appears to be the most rigidly stereotyped. There are several rapid peaks and the display is over. There are never any long pauses. Figure 6E illustrates an example of this head bob. Thirty-two head bobbing sequences were filmed, the number of peaks per sequence ranged from 2-5 (mean 4), and the time interval in frames ranged from 6-14 (mean 10.6).

Although in blood proteins *extremus* seemed to be intermediate in this series of three forms, in head bobbing, *roquet* and *aeneus* are more similar to each other than to *extremus*. Both forms have displays characterized by a long pause; thus the total time interval of the bobbing sequence is longer than that of *extremus*. *A. r. roquet* tends to have more peaks than does *aeneus*, while *aeneus* tends to have longer pauses and thus a longer bobbing sequence. However, there is considerable overlap, as tabulated:

Rapid bob		No. peaks		Total time of bob sequence (sixteenths of a sec.)	
	no.	range	mean	range	mean
aeneus	(25)	2-4	2.8	27-62	44.6
roquet	(28)	2-9	4.3	18-47	33.3

Figures 6A and RO compare rapid bobs in the two forms.

The examples depicted accurately show the typical differences in the head bobbing sequences between the two forms. Not only are there fewer peaks and a longer pause in *aeneus*, but it also may be seen that in the typical display of *aeneus* a head rise follows the drop after the long pause, whereas in *roquet*, following the long pause the head is dropped and the bobbing sequence is terminated.

A. trinitatis is the presumed ancestor of this group. Chromosome loss being rare, it is highly probable that *trinitatis* gave rise to only one of these forms. Two alternatives are plausible.

1. Colonization of Barbados, loss of chromosome pair, giving rise to *extremus*. *A. r. extremus* then sends out two radiations, one to Martinique where a transferrin difference evolves (*roquet*), the

other to Grenada where a new hemoglobin evolves (*aeneus*). The display of *extremus* is not very different from that of *trinitatis*. Both have head-bob sequences consisting of several peaks in a short time interval. The sequence of *trinitatis* is more variable, in both number of peaks and time interval and is occasionally punctuated by pauses. The similarity in display of *roquet* and *aeneus* would have to be accounted for by convergence.

2. Colonization of Grenada, loss of a chromosome pair, giving rise to *aeneus*. Evolution of the *aeneus* type display (increase in tendency for long pause, decrease in number of peaks) is followed by colonization of Barbados (*extremus*), and from there colonization of Martinique (*roquet*). There would be minor change in the head-bob display of *roquet*, and evolution of a new head-bob display in *extremus*.

There is one other bit of behavioral evidence that can be examined to assess these two alternatives. Members of the *roquet* group have a movement which I termed "rhythmic motion." This may consist of bobbing, or walking, or climbing in a very jerky manner. The animal will move, pause, move, pause, etc. The pause is long and the movement is very sudden and exaggerated. The actual context of the display is not fully understood by me, but it appears to occur at a somewhat lower intensity than the tail movements and the rapid head bob in male-male territorial encounters. This movement was seen most frequently in *extremus* and *aeneus*, but was also filmed occasionally in *trinitatis* and *roquet*.

In *A. r. extremus*, in eleven different displays, 100 intervals-between-bobs were measured. The range in frames (one frame = 1/16 sec.) was 5-12 (5-9 in 97 per cent of the intervals) and the mean interval between bobs is 7.27.

In *A. trinitatis* in four displays (from same individual) 30 intervals range from 7-11 with a mean of 8.46 frames.

In *A. r. roquet* only one sequence was filmed; there are 21 pauses ranging from 7-9 frames with a mean interval of 7.75.

In *A. aeneus* in ten displays 103 intervals were measured ranging from 9-19 frames with a mean of 11.9.

If this character has any meaning in terms of relationships, it implies that *aeneus* is the most divergent member of the series and that *trinitatis* is closer to *extremus*. This supports the first alternative above.

Table 1 (p. 29) summarizes some of the data for the *roquet* group.

DISCUSSION

At the level of the species group, the display behavior is useful as an additional taxonomic character. The *roquet* group can be defined as distinct from its geographic near neighbors by the absence of dewlap pumping within a display sequence. Furthermore, differences can be delineated which distinguish the eight forms of the species group.

Why stereotyped displays in island races of lizards? Why interisland differences? Do they relate to isolating mechanisms? Among some well-established cases of vocalization in birds, island races may have much more variable, less stereotyped, and less complex calls than the corresponding mainland races (Marler, 1959). The assumption here is that there are fewer sympatric congeners, and that there is therefore reduced selection for specificity.

The few studies on island lizards, however, do not show a similar pattern. The display of *Anolis townsendi,* a species restricted to Cocos Island some hundreds of miles west of the Central American mainland, is quite stereotyped (Carpenter, 1965). Furthermore, Carpenter (1966) found, in a study similar to this one, that 11 of 12 Galapagos islands have iguanids of the genus *Tropidurus* with species-specific (or island-specific) display patterns. Each island has only one *Tropidurus.* These differences were attributed to genetic drift.

In the study by Ruibal (1967) on comparative anole behavior, island races were discussed, but the species studied were from Greater Antillean islands where each species might have a half dozen sympatric congeners at the same locality. Yet the displays described are no more stereotyped than the ones described here.

It could be argued that some of the sympatric *roquet* group anoles evolved behavioral differences as additional isolating mechanisms. For example, there was double colonization of St. Vincent from St. Lucia, which led to *trinitatis* and *griseus.* Perhaps some of the differences in the displays as seen today reflect selection for species-specific differences.

Why are the displays no less stereotyped where there is only one form on an island? Probably the least variable display in the *roquet* group is that of *extremus* from Barbados, an island which has and probably has always had only one *Anolis.*

I have attempted to emphasize that certain components in the display of each form characterize that form, yet there is some variation in the temporal sequence of displays. Since each island was colonized by a presumably small number of arrivals from

another island, population differences in display are not at all surprising. There is sampling error to begin with. Then, as the new population adjusts to the new island, there is reconstruction of the gene pool. Displays are almost certainly polygenic, virtually all genes have pleiotropic effects, and thus differences in challenge displays in anoles on isolated islands are the expected result.

But selection, too, could be playing a very strong role. When we look at the display of *A. chrysolepis* and compare it with the *roquet* group, we find few similarities. *A. chrysolepis* hardly moves its body, but flashes its cherry-red dewlap quickly; in the *roquet* group the tail is waved, the head is bobbed, and there are vigorous push-ups.

When we look at the ecology of these anoles, this behavior makes perfect sense. *A. chrysolepis* is a small brown forest anole living in deep shade. Body movements would not be conspicuous, the wind might be rustling leaves. But a sudden flash of red color appearing from "nowhere" is quite striking. Anoles in the *roquet* group are larger and display from more open sites. Thus head and body movements are conspicuous sign stimuli.

At a subtler level, this line of reasoning could account for display differences within the *roquet* group. The islands are by no means identical. Bonaire, for example, is sparsely vegetated, St. Lucia has more characteristic lush tropical flora. Could differences in the configuration of the habitat act to select for display differences? In all probability they could. Perhaps it is advantageous for *luciae* to repeat himself by giving multiple head-bobbing series while a single long series suffices in the more open terrain for *A. bonairensis*.

In cases of sympatry in the Lesser Antilles, display differences may be very important in sexual selection, even though these displays are "territorial," not "courtship," displays. In a study of two sympatric species of grackles, Selander and Giller (1961) found that males hold mutually exclusive territories and solicit nesting females of either species. It is the females that must select conspecific mates based upon a display difference. Possibly, in *Anolis*, females associate only with males giving the "proper" display. Hunsaker (1962) showed that female *Sceloporus* preferentially associated with mechanical models which gave the species-specific head-bob. Because of the importance of display in the social structure of the population, even on a one-anole island we must expect limited variation, *i.e.* stereotypy.

Despite differences in displays of all the forms considered, it should be emphasized that the basic display patterns are quite

similar and that this may be used as a valuable taxonomic character. Quite possibly, in the Greater Antilles where 20 or more species of *Anolis* may be found on a single island, there might be very strong selection for behavioral differences (including challenge display) as isolating mechanisms in closely related forms. This would render the patterns taxonomically useless, except to show that different species had different displays: it would mask, rather than elucidate patterns of relationship.

In general, the behavioral data support my proposed phylogeny of the *roquet* group based upon chromosomes and proteins. The presumed prototype, *A. luciae*, has a display which could well be the basis for further elaborations and foreshortenings, leading to the displays of the other forms. It is interesting that *luciae* and *griseus* have very similar displays, which differ from *richardi*. An entirely different approach, marshalling biochemical evidence, has led me to the conclusion that *richardi* had to be derived from *griseus* and not vice-versa (Gorman and Atkins, 1968).

The relationship between *luciae* and *bonairensis* is less clear. If *blanquillanus*, the presumed intermediate, had been available for study, this perhaps could have been clarified.

Relating *trinitatis* and *luciae* closely is not a novel idea. Underwood (1962) considered them conspecific, although his reasons were not particularly clear. The two forms differ considerably in blood proteins; however, the similarity in karyotype and certain similarities in display behavior tend to support the idea of close relationship.

To compare the different island forms I have presented the data in an oversimplified manner. That is, I implied that a display once established is static. Thus, I call *luciae* ancestral to various other forms and compare the displays of today's *luciae* to the presumed derived forms. Obviously, the displays of all forms living in isolation are subject to change. The minor use of the tail in *luciae* may well be a secondary loss rather than a primitive character that was later elaborated in all the other members of the species group.

Despite the oversimplification, however, comparative behavioral data when combined with other information are valuable in tracing the evolution and relationships of the *roquet* group.

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TABLE 1

Head bob patterns of *roquet* group anoles

	Peaks/Bobbing Sequence			Time Interval in 16ths of Sec.	
Form	No. filmed sequences	Range	Mean	Range	Mean
luciae[1]	83	1-18	5.2	2-47	18
bonairensis[2]	14	12-23	17.7	43-95	62.2
bonairensis[3]	6	13-24	17.7	47-91	69.0
trinitatis	30	2-10	5.7	12-31	23.0
griseus[1]	18	1-8	3.3	1-41	16.6
richardi	8	4-7	5-8	39-58	47.3
extremus	32	2-5	4.0	6-14	10.6
aeneus	25	2-4	2.8	27-62	44.6
roquet	28	2-9	4.3	18-47	33.3

[1] In *luciae* and *griseus*, a head bobbing sequence consists of several series of bobs, with pauses between the series. These data are for the individual series.

[2] In *bonairensis* there are occasionally paused displays, as in *luciae* and *griseus*. Here are tabulated non-paused displays.

[3] This tabulates individual series of the paused displays.

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BREVIORA

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THE GENERA OF PUFFBIRDS (BUCCONIDAE)

G. W. Cottrell

In 1882, in the last part of *A monograph of the jacamars and puff-birds,* pages xxxiv-xli, P. L. Sclater divided the family of puffbirds (Bucconidae) into seven genera: *Bucco, Malacoptila, Micromonacha, Nonnula, Hapaloptila, Monacha* (Sclater's emendation of *Monasa* Vieillot 1816), and *Chelidoptera.* The large genus *Bucco,* containing twenty of the forty-three species enumerated for the family, he grouped in two subgenera (following Wagler 1827, *Systema avium*): *Bucco,* "rostro rotundato ad basin dilatato" (fifteen species), and *Nystalus,* "rostro compresso et magis elevato" (five species). He saw no grounds for division into subfamilies.

By 1914 the trend of the times had swelled the number of genera to thirteen, as set forth by Ridgway in *The birds of North and Middle America* 6: 371-373, the increment all taking place within the limits of Sclater's genus *Bucco.* The roster in Ridgway runs *Notharchus,*[1] *Argicus, Nystactes, Bucco, Hypnelus, Ecchaunornis,*

[1] Misprinted *"Northarchus"* in the key to the genera, *"Notharchus"* elsewhere. This name, with two of its trivial adjuncts, has had an ill-starred orthographic career. In 1958 Eisenmann, *Auk* 75: 101, called attention to the misprinting in Peters 1948, *Check-list* 6: 10, of the subspecific *hyperrhynchus* (Sclater 1856) as *"hyperrynchus."* And Ridgway's *"Northarchus"* has just been noted. But there is worse to come. In recent decades (first observed in Griscom 1932, *The distribution of bird-life in Guatemala*), *Notharchus* has frequently been printed *"Notharcus,"* contrary to the original publication, with indicated derivation, of Cabanis and Heine 1863, *Museum Heineanum* 4, 1: 149 (*Northarchus* formed from *νώθης*, sluggish, slothful, and *ἀρχός*, leader, chief — though the latter incorrectly accented *ἄρχος* by Cabanis and Heine). Of less consequence than the generic misspelling is the shift (dating back at least to Wagler 1827, *Systema avium*) of the ending of the specific name *macrorhynchos* as first published by Gmelin 1788, *Systema naturae* 1, 1: 406, from *-os* to *-us,* latterly perhaps by attraction to Sclater's *hyperrhynchus,* originally a specific designation but a subspecies of *macrorhynchos* since 1939 (Sassi, *Temminckia* 4: 161).

Nystalus, Malacoptila, Micromonacha, Hapaloptila, Monasa, Nonnula, Chelidoptera. The first seven genera (comprising Sclater's *Bucco*) are grouped as the subfamily Bucconinae, the remaining six as the subfamily Malacoptilinae. Cory 1919, *Catalogue of birds of the Americas* 2, 2: 390-410, has the same thirteen genera as Ridgway, but without division into subfamilies.

Thirty years later the emphasis in classification had shifted from dissimilarity toward similarity: Peters 1948, *Check-list* 6: 10-24, reduces the seven genera equated by Ridgway with Sclater's *Bucco* to four, *Argicus* and *Nystactes* being merged with *Bucco,* and *Ecchaunornis* with *Nystalus.* The other six genera remain unchanged. No subfamilies or subgenera are recognized. Peters' arrangement has been regularly followed down to the present (e.g., de Schauensee 1966, *The species of birds of South America*).

A new review of the family has led to the conclusion that a full return to Sclater's generic system should be made by merging *Notharchus, Nystalus,* and *Hypnelus,* maintained by Peters, with *Bucco.*[2] Since the *Check-list* does not justify its systematics, one must revert to Ridgway for criteria of differentiation. Ridgway follows Sclater in dividing his subfamily Bucconinae (Sclater's genus *Bucco*) into two major groups: one with thick bill, "its width at nostrils nearly to quite equal to its depth at same point" (Sclater's subgenus *Bucco*), the other with compressed bill, "its width at nostrils much less than its depth at same point" (Sclater's subgenus *Nystalus*). In the thick-billed group he included his genera *Notharchus, Argicus, Nystactes,* and *Bucco,* in the compressed-billed group the genera *Hypnelus, Ecchaunornis,* and *Nystalus,* paralleling Sclater's division except with respect to the species included in *Hypnelus,* which were placed by Sclater in the thick-billed group. An actual check of specimens shows the amount of compression to be only very slightly greater in Sclater's subgenus *Nystalus* (most in *maculatus*).

Lesser criteria of differentiation in Ridgway relate to variations in bill shape and color, tarsus length, length of rictal bristles, length of remiges or rectrices, plumage markings, as set out in his

[2] This same merging of genera was proposed and followed by Charles G. Sibley in a seminar syllabus on the Piciformes, Cornell University, ca. 1956, but was not published. Its actual priority is hereby duly recorded.

key.[3] Thus, *Notharchus* is distinguished from *Argicus, Nystactes,* and *Bucco* by tarsus shorter than outer anterior toe without claw, upper parts mostly plain blackish, forehead sometimes white, as opposed to tarsus equal to or longer than outer anterior toe without claw, upper parts mostly brown or rufous-tawny, forehead never white. We have seen that Peters included *Argicus* and *Nystactes* in *Bucco.* Within his compressed-billed group, Ridgway distinguishes *Hypnelus* from *Ecchaunornis* and *Nystalus* by a strongly bifid maxilla (see below), longer rictal bristles, longest primaries decidedly longer than secondaries, indistinct spotting of upper parts, black pectoral band, plain (unbarred) tail, wholly black (not red, orange, or horn) bill. Peters merged *Ecchaunornis* with *Nystalus.*

Such morphological criteria, as employed by Ridgway for his seven genera, and tacitly maintained by Peters for the four genera recognized by him, do not seem adequate for separation at the generic level. With respect to ethology, there are no recorded aspects that militate against the proposed merging — though information is in general scanty and fragmentary (also repetitious), and in some species almost totally lacking.

The genus *Bucco,* now re-extended to Sclater's limits (and equivalent to Ridgway's subfamily Bucconinae), is marked by a relatively stout and straight bill, much broadened at the base, with strongly uncinate tip to the maxilla and terminally ascending more or less convex gonys. A striking feature, found to greater or less degree in all but one of the species, is the bifid tip to the maxilla. An examination of specimens shows that this peculiar process, part of the rhamphotheca and not of the underlying bone, is particularly prominent in *tamatia* and *ruficollis* (including *bicinctus,* Phelps and Phelps 1958, *Proc. Biol. Soc. Wash.* 71: 122), pronounced in *macrorhynchos, pectoralis, ordii, tectus, noanamae, striolatus,*

[3] Ridgway's key cannot be relied on even within its own frame of reference. There is, for example, no subdivision "bb" to match "b" under "aa," which renders subsequent allocations indeterminate. The genus *Hapaloptila* appears under the subdivision "aa," characterized as having the tip of the maxilla not uncinate, whereas in fact the tip in *Hapaloptila* is strongly hooked. According to the key the bill in *Monasa, Nonnula,* and *Chelidoptera* is red, orange, or yellow, true in reality of *Monasa* only. Again, *Chelidoptera* is keyed as not "tawny" beneath, though actually with cinnamon-chestnut belly.

maculatus, fairly slight in *capensis,* slight in *radiatus,* very slight in *chacuru,* and not distinguishable at all in *macrodactylus.* In a study of this bifid process, Boetticher 1936, *Festschrift zum 60. Geburtstage von Professor Dr. Embrik Strand* 1: 74-77, suggested that it might serve as a sort of vise for holding the heads of captured flying insects (especially butterflies) while the wings were sheared off by the mutually adapted tomia. He admitted that there were no specific observational data to support his hypothesis; nor have any been reported since.

The treatment of this character in Ridgway is inconsistent and in part inaccurate (notably with regard to extralimital taxa). In the key there is the general statement, applicable to all seven genera, that the tip of the maxilla is sometimes cleft medially, but no discrimination between individual genera (and hence species) until the compressed-billed group, comprising *Hypnelus, Ecchaunornis,* and *Nystalus,* is reached. Here *Hypnelus* (consisting of the currently recognized *ruficollis*) is correctly signalized as having the tip of the maxilla strongly bifid, and *Ecchaunornis* (consisting of *radiatus* and *chacuru*) equally correctly as having the tip not distinctly if at all bifid. But *Nystalus* (consisting of *striolatus* and *maculatus*) is united in this respect with *Ecchaunornis,* whereas in actuality the medial cleft is pronounced in its component species. The subsequent generic description for *Notharchus* (consisting of *macrorhynchos, pectoralis, ordii,* and *tectus*) includes a more or less distinctly bifid tip to the maxilla, but there is no later indication as to the situation in *Argicus* (*macrodactylus*), *Nystactes* (*tamatia*), or *Bucco* (*noanamae, capensis*), descriptions being omitted for extralimital genera.

A review of the remaining six bucconine genera as found in Sclater, Ridgway, and Peters reconfirms their distinctness. They all have a less stout, more compressed, less basally broadened bill than the reconstituted *Bucco,* with the gonys more or less decurved terminally and, except in *Hapaloptila,* the maxilla more gradually decurved and non-uncinate. In none of the six does the bifid maxilla occur. Differences in size, in shape and proportions of bill, wings, and tail, and in plumage patterns serve adequately to separate one from another, as described and illustrated by Sclater, and hence are not detailed here. Certain ethological features reinforce the morphological distinctions, as may be seen in the social behavior of *Monasa* and the mode of flight and flocking of *Chelidoptera,* this latter being in many respects the most divergent of the taxa included within the family.

Consequent upon the merging proposed above, the genera and species of the Bucconidae stand as follows (order from Peters, species as in Peters except as indicated, subspecies not shown):

Bucco macrorhynchos, pectoralis, ordii, tectus, macrodactylus, tamatia, noanamae, capensis, radiatus, chacuru, striolatus, maculatus, ruficollis (includes *bicinctus* of Peters, following Phelps and Phelps 1958, *Proc. Biol. Soc. Wash.* 71: 122)

Malacoptila striata, fusca, semicincta (subspecies of *fusca* in Peters; distinct species here, following Traylor 1951, *Fieldiana, Zool.* 31: 614), *fulvogularis, rufa, panamensis, mystacalis*

Micromonacha lanceolata

Nonnula rubecula, sclateri, brunnea, ruficapilla (includes *frontalis* of Peters, following de Schauensee 1946, *Not. Nat.* 163: 5), *amaurocephala*

Hapaloptila castanea

Monasa atra, nigrifrons, morphoeus, flavirostris

Chelidoptera tenebrosa.

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BREVIORA

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THE STATUS OF *NESOGALAXIAS NEOCALEDONICUS* (WEBER AND DE BEAUFORT) (PISCES, GALAXIIDAE)

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ABSTRACT

The validity of the genus *Nesogalaxias,* proposed by Whitley (1935) for *Galaxias neocaledonicus* Weber and de Beaufort (1913), is supported by its very reduced pleural ribs, a character which has not been observed in other galaxiids. *N. neocaledonicus* occurs in mountain lakes in southern New Caledonia and is the most tropical species in the family. It is thought to have dispersed from Australia to New Caledonia when temperatures were lower during the Pliocene and Pleistocene, and the post-Pleistocene warming seems to have confined it to a few mountain lakes. Hitherto recorded only from Lac en Huit, *N. neocaledonicus* is now also known to occur in Grand Lac.

INTRODUCTION

In 1913, Weber and de Beaufort described a small fish species in the genus *Galaxias* from a lake in the mountains of southern New Caledonia. Several workers, e.g. Whitley (1935) and Scott (1936, 1966), have listed this species or commented on its generic position, but none appears to have re-examined it thoroughly. Since its generic status is currently uncertain, a re-examination of the species is necessary.

[1] Present address.
[2] On leave. Fisheries Research Publication No. 105.

In 1964, Dr. P. H. J. Castle collected a small sample of this species from Lac en Huit, the type locality, and more recently (1966), Mr. W. Skrzynski collected further samples from this lake, and also from Grand Lac, apparently for the first time. These samples have been generously made available to me, enabling an assessment of the affinities of this species to be made.

GENERIC STATUS

Although Whitley (1935) proposed a new genus for *G. neocaledonicus,* he supplied no generic diagnosis, merely stating that "it is not a true galaxiid and may receive the new generic name *Nesogalaxias.*" Scott (1966) found that "no feature in the original description would seem to preclude attribution to *Galaxias*" but apparently not having specimens, he took no further action.

Nesogalaxias is correctly included in the family Galaxiidae, its lack of scales, fin positions, lateral line pores on the head, dentition, lack of a mesocoracoid, and jaw structure all conforming to the general galaxiid pattern. *N. neocaledonicus* was found to come within the range of variation of members of the family in New Zealand, in most of the characters examined. Superficially it differs little from some of the more generalized species of *Galaxias.* Stokell (1945) revised the generic classification of the Galaxiidae. He suggested that the very long head of the specimen figured by Whitley (1935) indicated deformity and classed the genus as "not recognised."

However, Stokell's (1945) conclusion that the very long head in Whitley's (1935) figure is a deformity is incorrect, as the species does have a very long head (see Table 1). The pelvic fins have more posterior insertion than in most galaxiids, but this is a result of the great head length contained in the pre-pelvic dimension. In ratios of both standard length/head length and standard length/pre-pelvic length *N. neocaledonicus* represents an extreme for the family, but the range of values overlaps the ranges for these ratios in other species, e.g. *Galaxias argenteus* (Gmelin). Vertebral number (41-43) is very low, but not as low as in *G. zebratus* (Castelnau), which Jubb (1965) reported as having 39-41 vertebrae.

In most osteological characters, *N. neocaledonicus* is conventional for the family Galaxiidae. The caudal skeleton shows the

irregular variability which is characteristic for the family, and is not distinctive. The pectoral girdle lacks the postcleithrum, but this bone has disappeared in several other unrelated species, e.g. *G. divergens* Stokell, *G. paucispondylus* Stokell. However, in the absence of pleural ribs from those vertebrae behind the pelvic fins, *N. neocaledonicus* is different from all other galaxiids examined. These bones are present on vertebrae between the head and about the level of the pelvic fins, but thereafter disappear quite suddenly from the remainder of the abdominal vertebrae. The ribs present anteriorly, although short, are well developed, appear to be strongly ossified and have well developed heads articulating with the parapophyses of the vertebrae. There are no epipleural ribs. The habits of *N. neocaledonicus* are somewhat different from other galaxiids (see p. 5) and this species seems to have entered a somewhat unusual type of niche for the family. These characters suggest that *N. neocaledonicus* stands apart from the rest of the family Galaxiidae and is best regarded as generically distinct from the more generalized species. The name *Nesogalaxias* Whitley (1935) has priority and is available.

Nesogalaxias Whitley, 1935

Type species: *Galaxias neocaledonicus* Weber and de Beaufort, 1913, by original designation.

Diagnosis: Trunk cylindrical to a little compressed, naked, dorsal fin posterior, above vent. Pelvic fins present, usually seven rayed. Caudal fin forked with 16 principal rays. Teeth uniserial on jaws and entopterygoids, biserial on basihyal. Postcleithrum absent. Pleural ribs lacking from abdominal vertebrae behind the pelvic fins.

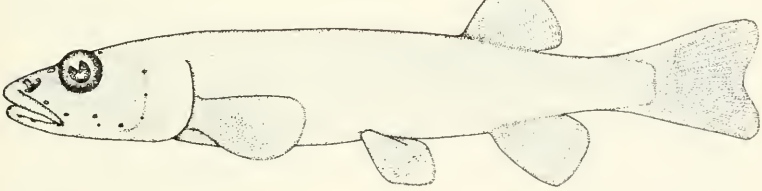

Figure 1. *Nesogalaxias neocaledonicus* (Weber and de Beaufort, 1913). Lac en Huit, New Caledonia. Length to caudal fork 52 mm.

NESOGALAXIAS NEOCALEDONICUS (Weber and de Beaufort, 1913)

Galaxias neocaledonicus Weber and de Beaufort, 1913: 173.
Nesogalaxias neocaledonicus, Whitley, 1935: 42; Scott, 1936: 85, 1966: 250.

Syntypes: Zoology Museum, Amsterdam, Holland, no. ZMA 104, 700, 2 specimens (seen). Muséum National d'Histoire Naturelle, Paris, France, nos. 2312-3 (Bertin and Esteve, 1951, not seen).

Type locality: Recorded as "Lac en 8, sudliches Neu-Kaledonien" by Weber and de Beaufort. The locality for the paratypes in the Muséum National d'Histoire Naturelle is listed as "Lac en Huit" by Bertin and Esteve (1951).

Description (Fig. 1, Table 1): A small, rather slender species, trunk deep anteriorly but tapering to a very slender caudal peduncle which is much longer than deep. Greatest body depth somewhat behind pectoral fin bases. Head very long, slender, flattened ventrally, tapering rather abruptly forward dorsally to a slender, long snout. Eye large, projecting above head profile, interorbital concave, very narrow. Jaws sub-equal, long, extending to about anterior third of eye, gape narrow. Profile of lower jaw from ventral aspect deep and U-shaped. Canine teeth weakly developed in jaws; three to four moderately developed entopterygoidal teeth. Gill rakers strongly developed; two weak pyloric caeca.

Dorsal and anal fins membranous and short based, rather high. Anal origin a little behind a line through dorsal origin. Pectoral fin inserted rather low, long in interval between pectoral and pelvic fin bases. Pelvic fin long in interval between pelvic base and anal origin, fin tapering to a point medially with middle rays longest. Caudal fin forked, rather short, fin tips rounded; flanges of caudal peduncle rather poorly developed.

Size: Weber and de Beaufort listed a maximum size of 76 mm in their sample. Amongst fishes examined by the writer, the largest was only 56 mm long, and most adults and sub-adults were 40-50 mm long.

Coloration: Trunk a uniform grayish brown, darkening dorsally and on head; ventrally paler, creamish gray. Pigmentation extends a little on to bases of fins, especially the caudal.

Meristic variation: Dorsal fin rays (segmented) 8 (6), 9 (12) 10 (2); anal rays 9 (2), 10 (14), 11 (4); caudal rays (principal) 15 (1), 16 (19); pectoral rays 11 (5), 12 (14), 13 (1); pelvic rays 6 (1), 7 (19); branchiostegals 6 (7), 7 (13); vertebrae 41

(3), 42 (16), 43 (3); gill rakers 3-11 (1), 3-12 (0), 3-13 (3), 4-11 (1), 4-12 (6), 4-13 (4), 5-12 (1), 5-13 (3), 6-13 (1).

DISTRIBUTION AND HABITAT

N. neocaledonicus is known only from two small lakes in the Plaine des Lacs, New Caledonia (Fig. 2) — Lac en Huit and Grand Lac. Skrzynski (personal communication) has kindly supplied the following notes on the lakes and the habitats in which he found this species.

The Plaine des Lacs is about 100 km from Nouméa. There are two main lakes, Lac en Huit and Grand Lac, each at an altitude of about 250 m, and a few square kilometers in area. They are about 1½ km apart and separated by a ridge, their outflows merging a few kilometers below the lakes.

Both lakes are depressions in an iron pan, their bottoms being solid rock with loose rock and soil in some places. The only aquatic plant growth observed consisted of loose patches of reeds in a few areas and encrusting algae. Neither of these provide much cover for fishes and the only cover in which *N. neocaledonicus* was observed was loose rock on the lake bed and crevices in the bed itself. The fish were found to conceal themselves in this cover during the day, but at night were commonly observed swimming in mid-water. Small unpigmented juveniles about a centimeter long were found to shoal freely in mid-water during the day.

RELATIONSHIPS AND ORIGIN

N. neocaledonicus is the most tropical species generally recognized as a galaxiid. *G. indicus* Day, from India, has not been recollected since it was first described in 1888, and is doubtfully a galaxiid. Apart from *N. neocaledonicus* and the doubtful *G. indicus,* fishes of this family are confined to the southern temperate zone and, like the Northern Hemisphere salmonoids, are primarily cold water fishes. The fact that *N. neocaledonicus* has found refuge in the mountain lakes of New Caledonia suggests that it too prefers or is limited to cold waters. If this is so, it seems probable that it reached New Caledonia at a time of cooling, most likely in the Pliocene-Pleistocene, when lowered temperatures would have facilitated dispersal to New Caledonia. With subsequent postglacial warming occurring, the populations have become confined to the cooler mountain lakes.

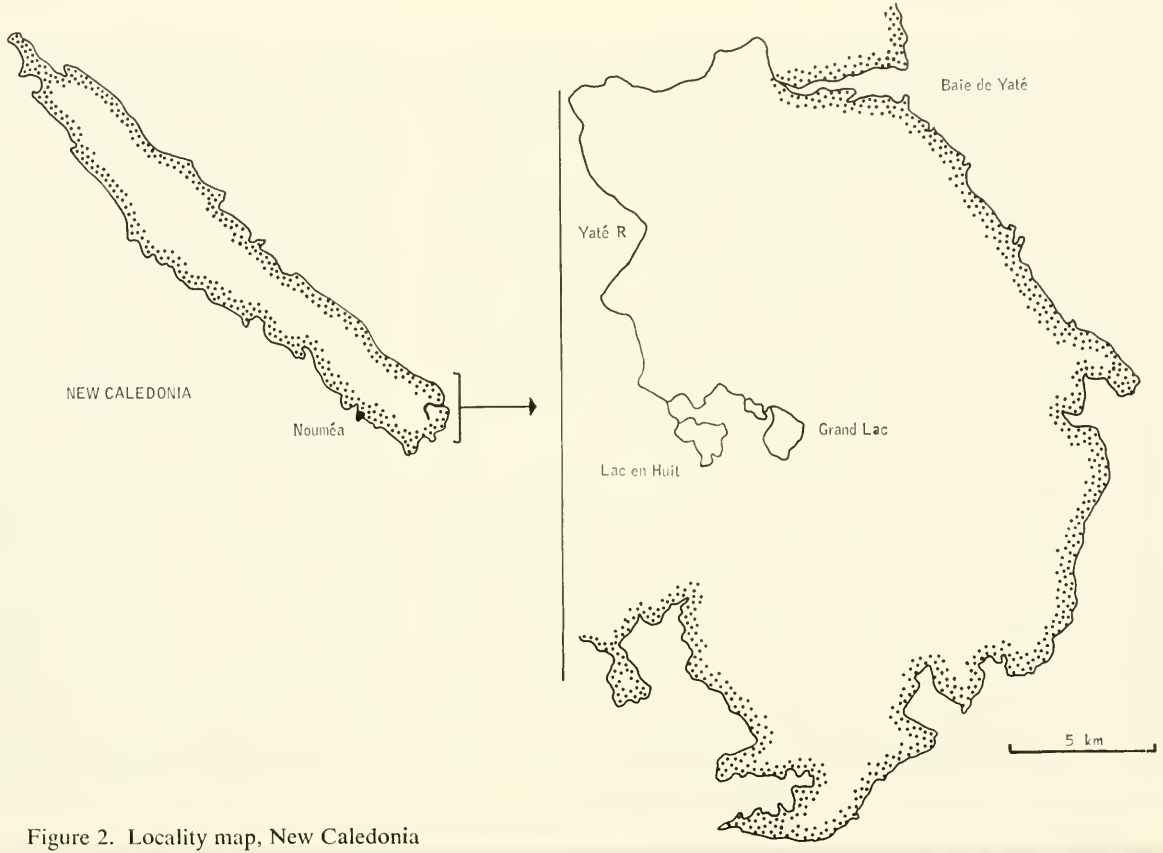

Figure 2. Locality map, New Caledonia

The relative closeness of New Caledonia to Australia points to likely origin of its galaxiid populations in Australia. To what species or species group in Australia *N. neocaledonicus* is most closely related is quite unknown, but it seems likely that its ancestor was diadromous, since oceanic dispersal would have been necessary for the fishes to reach New Caledonia. Analysis of the Australian galaxiid fauna may indicate the relationships of *N. neocaledonicus*.

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TABLE 1

Morphometric variation in 20 *Nesogalaxias neocaledonicus*.

	Min.	Mean	Max.
Length caudal fork/standard length	1.07	1.12	1.16
Standard length/body depth at vent	7.86	8.36	9.06
Standard length/length caudal peduncle	6.46	7.11	8.25
Length caudal peduncle/depth caudal peduncle	1.50	1.96	2.25
Standard length/pre-dorsal length	1.34	1.38	1.40
Pre-anal length/pre-dorsal length	1.03	1.05	1.07
Standard length/length dorsal fin base	8.95	10.36	12.33
Greatest length of dorsal fin/basal length	1.43	1.63	1.93
Standard length/length anal fin base	8.00	9.45	10.26
Greatest length of anal fin/basal length	1.36	1.59	1.82
Pre-pelvic length/standard length	0.53	0.56	0.59
Pectoral-pelvic length/standard length	0.24	0.27	0.28
Pectoral fin length/pectoral-pelvic length	0.57	0.62	0.70
Pelvic-anal length/standard length	0.20	0.22	0.23
Pelvic fin length/pelvic-anal length	0.55	0.66	0.72
Standard length/head length	3.04	3.23	3.39
Head length/head depth	1.96	2.19	2.45
Head length/head width	1.96	2.14	2.33
Head length/snout length	2.89	3.25	3.53
Head length/post-orbital head length	1.85	2.03	2.15
Head length/interorbital width	3.70	4.36	5.09
Head length/diameter of eye	4.45	4.91	5.45
Head length/length of upper jaw	2.42	2.65	2.83
Head length/length mandible	2.57	2.72	2.88
Head length/width of gape	2.89	3.66	4.08

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THE SEQUENCE OF GENERA IN THE ESTRILDIDAE (AVES)

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The manuscript for the list of the Estrildidae in volume XIV of Peters' Check-list of Birds of the World is being prepared by three authors, Melvin Traylor (Africa), R. Paynter (Oriental and Palearctic Regions), and myself (Papuan Region and Australia). The task of coordinating the three accounts was assigned to me. Since each species, with few exceptions, is restricted to a single geographical region, the main problem of coordination is the recognition of genera and the choice of a sequence. To have a widely acceptable sequence of genera is particularly important in view of the fact that members of this family are used increasingly for behavior studies and in physiological research.

Research on the classification of the Estrildidae has been very active in the last two decades, particularly since the publication in 1943 of Delacour's classical study. This was the first consistent attempt to arrange the genera in groups, and to utilize various biological characters (courtship, palate markings of the nestlings, etc.). The subsequent researches of Steiner, Wolters, Immelmann, Nicolai, and others, have all been endeavors to improve on the foundation laid by Delacour.

The ranking of the taxon Estrildidae and its delimitation from the Viduinae and the Ploceidae have been discussed by several authors. Until recently the estrildids were considered a subfamily of the Ploceidae. Delacour (1943) derived them from the Sporopipinae, and neither Chapin (1917) nor Sushkin (1924, 1927) questioned the close relationship of the weavers and estrildids. The realization has, however, grown in recent years that not all "finches" are necessarily a monophyletic assemblage, and that a cone-shaped bill may have been acquired independently in several groups of seed-eating birds. There is no a priori necessity for a close relationship between ploceids and estrildids. Steiner (1955) undertook a careful comparison of the two groups and concluded

that they differ in so many important characters that he questioned a close relationship. Some of these differences are valid only in a comparison of the Estrildidae and the Ploceinae (*sensu stricto*). The opinion has therefore been expressed, that the stated differences are only subfamily differences. It is still possible that the Ploceidae are the nearest relatives of the Estrildidae; nevertheless, the differences are numerous and striking. Estrildids and ploceids are clearly different in courtship posture, clutch size, egg coloration, pattern in mouth of the young, and mode of begging of the young. In an analysis of the structure of the digestive tract, Ziswiler (1967) comes to the conclusion that the Estrildidae are far more different from the Ploceidae than the ploceid subfamilies are from each other. The Viduinae, interestingly, agree in this character quite well with the other Ploceidae rather than with the Estrildidae. Africa is the home of the most primitive genera of estrildids and, presumably, the home of the family. It must be an old family, considering the subsequent rich radiation in the Australian Region. It is advisable for the time being to consider the estrildids a separate family, perhaps distantly related to the Ploceidae, but sufficiently distinct to deserve family rank.

The Viduinae are nest parasites of the Estrildidae and have generally been considered to be very closely related to them. The similarity in the palate pattern of the nestlings was undoubtedly the major reason for this opinion. Delacour (1943: 73) questioned this assumption: "As there exists no transition between [the Estrildinae and the Viduinae], it appears that their similarities are due to recent adaptation and I have come to the conclusion that the Estrildinae have probably evolved independently from the Sporopipinae, just as have the Viduinae and the Ploceinae." The fact that the nestlings of each *species* of *Vidua* have the palate markings of one particular species of waxbills clearly indicates convergence rather than common descent. In the meantime, Nicolai (1964) has demonstrated convincingly that the similarities between viduines and estrildids are due to nest parasitism. He has, in addition, produced evidence to indicate a derivation of the viduines from *Euplectes*. To indicate this relationship, the Viduinae should be treated as a subfamily of the Polceidae rather than of the Estrildidae. Sibley (MS) has discovered similarities in the starch gel patterns of viduines and Passerinae.

The valid name of the (sub-) family of the estrildids is still somewhat in doubt. The first available name for this taxon is apparently Spermestinae Cabanis (1847, Arch. Naturg., 13: 331, also 1851, Mus. Heineanum, 1, Singvögel: 172), based on the

generic name *Spermestes* Swainson 1837. This name has since been used occasionally, as in Gray, 1870 (Handlist Birds, 2: 49), Reichenow, 1904 (Vögel Afrikas, 3: 103), Steiner, 1960 (J. Ornith., 101: 92-112), and in some of the avicultural literature.

In the scientific ornithological literature the name Spermestinae has been almost completely displaced by the name Estrildidae. This name was apparently first proposed by Bonaparte, 1851 (Consp. Av., 1: 450) (erroneously spelled Estreldinae), based on the genus *Estrilda* Swainson 1827. Bonaparte's name, in its corrected spelling Estrildinae, is used in virtually all those modern standard works in ornithology, in which the (sub-) family is recognized as different from the Ploceidae. It is the name used by Stuart Baker (1926, Fauna Brit. India, Birds, 3: 77), Sclater (1930, Syst. Av. Aethiop., p. 769), Berlioz (1950, *in* Grassé's Traité Zool., 15: 1039), Chapin (1954, Birds Belgian Congo, 4: 451), and Ripley (1961, Synopsis Birds India: 602).

The name Estrildinae is likewise the name adopted by most modern revisers of the family, for instance by Delacour (1943, Zoologica, 28: 69), Wolters (1957, Bonn. Zool. Beitr., 8: 90-129), and Keast (1958, Emu, 58: 219-246). It is the name adopted in general classifications, such as Mayr and Amadon (1951, Amer. Mus. Novit., 1496: 38).

The name Spermestinae has presumably been rejected almost universally because the name *Spermestes* Swainson 1837, on which it is based, is considered by most modern authors to be a synonym of *Lonchura* Sykes 1832. If the name Spermestinae were restored, the valid name of the type genus of this subfamily would be *Lonchura,* an inconvenient lack of congruence. The name *Spermestes* has not even been used by recent authors for any of the subdivisions of the Estrildidae, the waxbills (Estrildae), the grass finches (Erythrurae or Poephilae), or the mannikins (Amadinae or Lonchurae).

It is clear that this is a situation to which Article 23d (ii) of the International Code is applicable. There is strong justification for the name Estrildidae to be placed on the Official List and the name Spermestidae on the Official Index.

Delacour's revision was followed by reviews of the family (or some of the species) by Desmond Morris (1954, 1958), Moynihan and Hall (1954), Wolters (1957), Steiner (1960), Hall (1962), and Immelmann (1962). Steiner, in particular, proposed a classification which differed drastically in many ways from that of Delacour. For the 108 (-110) species of the family, Delacour recognized 15 genera with a total of 26 subgenera (including the

nominate subgenera), while Steiner recognized 34 genera with 53 subgenera, and Wolters 31 genera with 62 subgenera.

It has become very evident that there is at present a real difference of opinion between the taxonomists and the ethologists concerning the size of genera. In recent years many species of estrildids have been kept in captivity and their courtship and other aspects of biology have been carefully analyzed. Through these studies the ethologists have discovered more and more behavior differences even between the most closely related species, and are therefore enormously impressed with the distinctness of every species (except a few sibling species or semispecies). As a consequence, they tend to admit numerous genera, many of them monotypic. For instance, Immelmann (1965) recognizes 13 genera for the 16 native Australian superspecies of estrildids (2 species have 2 semispecies each). Such an emphasis on distinction destroys the concept and function of the genus as a means of expressing relationship. Admittedly, there are some extremely distinct species which must be classified as monotypic genera, but for others it is much better to place them in the same genus with the most nearly related species. Recognition of subgeneric status is sufficient to bring out the proper level of distinctness.

The discrepancy between the various authors with respect to the sequence of genera is equally disconcerting. Although Delacour's sequence, waxbills, grass finches, and mannikins, has been, on the whole, adopted by most subsequent authors, there has been great variation in the sequence of genera within each subgroup, and in the assignment of certain genera, particularly *Aegintha, Amadina, Erythrura,* and *Chloebia,* to the three subgroups.

In an endeavor to achieve a reasonable consensus, I worked out a tentative sequence of recognized genera, and submitted it to the following specialists for their opinions: Collin Harrison, Klaus Immelmann, Allen Keast, Desmond Morris, J. Nicolai, Melvin A. Traylor, and H. W. Wolters. They responded most generously and supplied me with abundant details bearing on the question of relationship and the importance of various taxonomic characters. A revised sequence, prepared on the basis of this first set of answers, was circulated together with a questionnaire in which 19 specific questions were asked concerning sequence and the advisability of recognizing certain genera.

The present paper is the result of an analysis of this correspondence. It is obvious that relationships cannot be decided by majority vote, and yet I feel that an arrangement that has been reached in consultation with the active specialists has a greater prospect for

stability than an arrangement based on the opinions of a single worker. The following comments may be useful to other students of the Estrildidae. Publication of these notes at this time may stimulate further research that can still be utilized in the preparation of the manuscript on this family for Peters' Check-list of Birds of the World.

The Estrildidae appear to be unique among bird families in that color pattern is a relatively poor clue to relationship. On the other hand, courtship song (Hall, 1962) and display postures seem to have high taxonomic weight. As a consequence, a sorting of the species and genera on the basis of coloration leads to a classification which is flatly contradicted by various biological characteristics, including the palate pattern of the young. As in all weighting of taxonomic characters, there is an element of subjectivity in the decision to give higher weight to behavioral characters than to plumage pattern, yet this decision is supported in this family by a correlation among the various biological characters. The sequence here proposed is based on this correlation.

THE WAXBILLS (ESTRILDAE)

A glance at Delacour's diagram of relationships (1943, fig. 1) clearly shows the central position of *Clytospiza*. One might, therefore, start the sequence of genera with *Clytospiza* and follow it with the several derived sequences. However, this not only results in several breaks in the sequence, but it also removes *Clytospiza* far from the *Estrilda* group which also seems to be derived from a *Clytospiza*-like ancestor. Under the circumstances, it is better to adopt the following sequence: *Parmoptila, Nigrita, Nesocharis, Pytilia, Mandingoa, Cryptospiza, Pirenestes, Spermophaga,* and *Clytospiza*. This arrangement differs from that of Delacour in two significant respects: *Nesocharis* Shelley is considered a valid genus, probably related to *Nigrita; Mandingoa* (*nitidula*) is considered related to *Cryptospiza* rather than to *Hypargos*. All 9 genera are well defined and form a primitive group among the waxbills, a group on the whole more closely associated with bushes or forest than with grass. "I place *Nesocharis* near *Nigrita* to which it has some similarity in mouth markings and habits, but affinities with *Nigrita* are by no means certain. However, I can find no better place for this very distinct, tit-like genus" (Wolters *in litt.*).

There is comparatively little argument about the *Estrilda* group among the waxbills, except on the number of valid genera. Delacour placed all species in *Estrilda* (and *Hypargos*), while Steiner,

Wolters, and Immelmann would like to recognize a minimum of 8 genera, probably best arranged in the following sequence: *Hypargos, Euschistopiza, Lagonosticta, Uraeginthus* (= *Granatina*), *Estrilda, Ortygospiza, Amandava* (incl. *Sporaeginthus*), and *Stictospiza*. Two pairs of these "genera" are rather close to each other, and it may result in more equal standards when *Lagonosticta* and *Uraeginthus* are combined, and also *Amandava* with *Stictospiza*. "*Uraeginthus* is closer to *Lagonosticta* than to *Estrilda* with which it has been merged by several authors" (Wolters *in litt.*). *Estrilda, Lagonosticta,* and *Uraeginthus* have been lumped at various times or split more finely. *Estrilda* and *Lagonosticta* seem sufficiently different in song and courtship to be maintained as two genera. *Uraeginthus,* on the other hand, is sufficiently closer to *Lagonosticta* than to *Estrilda,* that it might be treated only as a subgenus (Wolters, 1966). The species of this group are to be assigned as follows (not necessarily exactly in the listed sequence):

Estrilda

melanotis, paludicola, melpoda, rhodopyga, troglodytes, astrild, nonnula, atricapilla, erythronotos (+ *charmosyna*), *thomensis, perreini, caerulescens, rufibarba, nigriloris*

Lagonosticta, subg. *Lagonosticta*

larvata + *nigricollis* + *vinacea, rara, rubricata, rhodopareia* + *jamesoni, senegala, rufopicta, nitidula, landanae*

Lagonosticta, subg. *Uraeginthus*

bengalus, angolensis, cyanocephala, granatina, ianthinogaster.

Granatina (1850) would have one year priority over *Uraeginthus* (1851), if it were an available name. It was, however, published by Bonaparte in the plural as *Granatinae,* and is thus not available according to Article 11f of the Code. The subgenus has to be called *Uraeginthus.*

"The similarities between *Ortygospiza* and *Amandava* in plumage pattern, mouth markings, and behavior are so numerous that it would be difficult to believe that they should be due to convergence" (Wolters *in litt.*). *Ortygospiza* deserves only subgeneric status.

THE GRASS FINCHES (POEPHILAE)

Aegintha (*temporalis*) is a problem. On first sight, the Australian *temporalis* seems very close to the African *Estrilda* (e.g. *melpoda*), and this is where Delacour placed it. Yet, in its display and some other respects it seems close to the Australian *Emblema*

group and is placed with the Australian genera by Steiner, Immelmann, and Wolters. Others still think that the similarity to *Estrilda* is more than convergence. At present, it would seem best to place *Aegintha* in the grass finches, but closest to the waxbills. "*Aegintha* is the '*Estrilda*-type' among the Australian finches. Superficially, there is considerable similarity with African *Estrilda,* but the green of *Aegintha* is not found anywhere among the Estrildae (the kind of green in *E. melanotis* is quite different). The eyestripe is *above* the eye, not through the eye, and of a different red. The courtship has rather primitive aspects as in *Estrilda* and *Zonaeginthus,* and does not provide decisive information. I am not at all convinced of any close relationship between *Aegintha* and *Estrilda.*" (Immelmann, 9. IV. 1966 *in litt.*).

Delacour recognized only three genera, *Zonaeginthus* [=*Emblema*], *Poephila,* and *Erythrura.* All subsequent work has confirmed the naturalness of these three groups, but this is where the agreement ends. Steiner, for instance, splits *Emblema* into 7 genera (*Zonaeginthus, Stagonopleura, Emblema, Aidemosyne, Bathilda, Neochmia,* and *Oreostruthus*), all but *Zonaeginthus* (2 species) monotypic. *Aidemosyne,* as shown by recent researches (Steinbacher and Wolters, 1953 ff.; Keast, 1958; Morris, 1958; Immelmann, 1962), is close to *Lonchura* and must be shifted to the mannikins. The palate pattern is the only resemblance with the *Emblema* group. To split the remaining *Emblema* group into 6 genera seems excessive. Recognition of three genera, *Emblema* (with *Stagonopleura* and *Zonaeginthus*), *Oreostruthus* (the somewhat aberrant Papuan genus), and *Neochmia* (with *Bathilda*) would seem to give better balance.

There is great confusion about the nomenclatural validity of the generic names in the *Emblema* group. The name *Stagonopleura* was proposed by Reichenbach in 1850 for a bird of which a black-and-white drawing of head, legs, and tail is given. Subsequent authors have applied the name to various groups of Australian estrildines, but the combination of a gray (or at least dark) crown, black lores and eye patch, and light (?white) unmarked chin and throat occurs in only one species, the Diamond Firetail Finch (*guttata*). Cabanis was therefore quite right (1851, Mus. Hein., 1: 172) in designating *Loxia guttata* Shaw as type for "Reichenbach's genus." The name *Stagonopleura* (pleurae with drop-like spots) also fits this species excellently.

Bonaparte (1851, Consp. Av., 1: 456), even though crediting the name to Reichenbach, inadvertently misspelled it *Steganopleura* (covered-up or roofed-over pleurae), which makes no sense for

this species. This spelling does not constitute an available name, since it is clearly an "incorrect subsequent spelling" and not an "intentional emendation" in the sense of Article 33. As stated in the Code: "Any change in the spelling of a name, other than an emendation, is an 'incorrect subsequent spelling'; it has no status in nomenclature and therefore does not enter into homonymy and cannot be used as a replacement name."

Ignoring the unavailability of this name, Mathews (1919, Birds of Australia, 7: 434) designated *Fringilla bichenovii* Vigors and Horsfield as the type of *Steganopleura* Bonaparte and used it for the group of species previously known under the generic names *Stictoptera* Reichenbach or *Stizoptera* Oberholser. This was clearly an invalid action.

For *Stagonopleura* of Reichenbach 1850, Mathews uses his own name *Tavistocka* 1919, while Delacour, Keast, and Immelmann use *Zonaeginthus* Cabanis 1851. Actually, as shown above, *Stagonopleura* continues to be an available name, but there is doubt as to its validity (see under *Emblema* below).

Keast employs a subgenus *Zonaeginthus* (*Emblema*), but since *Emblema* was proposed in 1842 and *Zonaeginthus* in 1851, it clearly will have to read *Emblema* (*Zonaeginthus*). Immelmann recognized *Emblema* as a separate genus from *Zonaeginthus,* which carries splitting rather far. For the closely knit group of species consisting of *pictus, oculatus, bellus,* and *guttatus* Shaw we have thus three generic names available: *Emblema* Gould 1842 (*picta*), *Stagonopleura* Reichenbach 1850 (*guttata*), and *Zonaeginthus* Cabanis 1851 (*bellus*), and the only remaining question is whether the name *Emblema* is valid or preoccupied.

Emblema Gould 1842 was in unchallenged use between 1842 and 1930, when Iredale (1930, Austral. Zool., 6: 175) contended that it was preoccupied by *Emblema* Deshayes 1840 (mollusks). He renamed it *Cayleyna.* Deshayes' name was neither an erroneous spelling of *Amblema* Rafinesque nor a valid emendation. When one looks up the original citation of *Emblema* Deshayes (1840, D'Orbigny's Dict. Univer. Hist. Nat. 1: 334), one finds that he mentions *Emblema* merely in a purely philological comment, as the correct transliteration of the Greek word from which it was derived, but lists his discussion under "Amblème (*Amblema*)." Since he does not adopt *Emblema,* this spelling cannot qualify as an emendation in the sense of Article 33. It is a spelling without nomenclatural status. It is fortunate for the stability of nomenclature that there are only a few authors who would use the flimsy excuse of

this philological discussion to upset the nomenclature of a well-known genus that had been totally stable for the preceding 88 years! Nor have the malacologists ever employed the version *Emblema*. Since 1914, the name *Amblema* Rafinesque has been used universally for the so-called washboard clams (type, *A. costata* Rafinesque, 1820) and there is not the slightest reason for suppressing *Emblema* Gould for fear that it might be confused with the molluskan genus *Amblema*. A recent Opinion of the Commission (not yet published) deals with this name. Since writing this, I have discovered that Mees (1961, J. Roy. Soc. West. Austr., 44: 123) had independently come to the same conclusions.

The complete synonymy of the genus *Emblema* is thus as follows:

Emblema Gould, 1842, Birds Australia, pt. VII. Type, by monotypy, *E. picta* Gould. [Not preoccupied by the nomenclaturally unavailable *Emblema* Deshayes 1840.]

Stagonopleura Reichenbach, 1850, Av. Syst. Nat., pl. LXXV. Type, by subsequent designation (Cabanis, 1851), *Loxia guttata* Shaw.

Steganopleura Bonaparte, 1851, Consp. Gen. Av., 1: 456. Nomenclaturally unavailable, as an "incorrect subsequent spelling."

Zonaeginthus Cabanis, 1851, Mus. Hein., 1:171. Type, by subsequent designation (Gray, 1855: 76), *Loxia nitida* Latham = *L. bella* Latham.

Tavistocka Mathews, 1919, Birds Australia, VII: 434. New name for *Stagonopleura* Reichenbach.

Cayleyna Iredale, 1930, Austr. Zool., 6: 175. New name for *Emblema* Gould.

The *Poephila* group is typical for the difficulties one faces in the grass finches. There are three fairly distinct species groups, containing species that "are highly specialized in color pattern and general proportions, and no intermediates exist between them. That is the reason why so many monotypic, and in my judgment utterly unnecessary genera have been created for them" (Delacour, 1943: 80). The behavior specialists, on the other hand, are impressed by the differences. I propose a compromise solution, in which two subgenera (*Poephila, Taeniopygia*) are recognized. The species *bichenovii* is not sufficiently different from *guttata* Vieillot to justify recognition of a third subgenus (*Stizoptera*). The grass finches *sensu stricto,* after the removal of *Erythrura* (see below), should be called the Poephilae, consisting of the genera *Emblema, Oreostruthus, Neochmia,* and *Poephila.*

THE MANNIKINS (LONCHURAE)

Gould's Finch (*gouldiae*), as shown by recent behavior studies (Wolters, 1950; Mitchell, 1958; Immelmann, 1959; and Steiner, 1960), does not belong in *Poephila.* It was first thought to fit into *Erythrura* but recent studies indicate similarities also with *Lonchura* (Nicolai MS; Hall MS; Immelmann, 1962). Recognition of the genus *Chloebia* (near *Erythrura*) for *gouldiae* would seem indicated until the situation is better understood. It is also now becoming clear that *Erythrura* is not really a grass finch, related to *Emblema-Poephila,* but that it is very distantly related to the *Lonchura* group. The *Erythrura* group is, however, very isolated.

"*Chloebia* shows a great deal of similarity with *Erythrura* in plumage color and mouth markings but reminds one in pattern also of some species of *Lonchura* (e.g. *castaneothorax*). In behavior it occupies an equally intermediate position, only there are more similarities with *Lonchura* than with *Erythrura.* The voice of *Chloebia* is typical for *Erythrura,* while the display is very similar to that of *Lonchura malacca, L. maja,* and *L. castaneothorax. Chloebia* sings with the same rigid posture and a pulled-in head as these species of *Lonchura,* but has retained a number of ancestral components of the Estrildidae courtship which have been lost by the *Lonchura* species, such as the hopping during the courtship dance. The species of *Erythrura* which I know best (*trichroa, cyanovirens, psittacea*) not only fail to carry grass stems during their display but even the dance itself has completely disappeared." (Nicolai, *in litt.*).

The precopulatory display of *Erythrura* is unique among the Estrildidae and resembles neither that of *Lonchura* nor that of any other genus. "*Erythrura prasina* is somewhat intermediate between typical *Erythrura* and *Chloebia* and since the latter has many similarities with *Lonchura,* I believe that it is best to place *Chloebia* between *Erythrura* and *Lonchura.*" (Nicolai, 4 August 1965, *in litt.*).

The mannikins are, on the whole, a homogeneous group. The only genera whose assignment to the Lonchurae can be questioned are *Amadina* and *Chloebia-Erythrura.* As far as the remaining species are concerned, there is only the question of the number of genera to be recognized. Are *Euodice, Odontospiza,* and *Spermestes* valid? *Spermestes* (and *Odontospiza*) have certain primitive traits, and so does *Euodice* (which Harrison, 1964, cannot confirm). Some recent authors recognize *Spermestes* as different from *Lonchura;* others, like Delacour, do not. Kunkel (1965) lists the behavioral differences, which to me do not seem to justify more than

subgeneric rank. The same is true for *Euodice*. *Odontospiza* deserves generic status even less and is best placed in the same subgenus (*Euodice*) as *malabarica-cantans*. The Java Finch (*oryzivora*) is so distinct that it is best recognized as a separate genus (*Padda*), even though admittedly *Padda fuscata* connects this genus with *Lonchura;* "*Heteromunia*" (*pectoralis*) is so close to *Lonchura,* particularly the *castaneothorax* group, that it cannot be recognized as a monotypic genus, even though it has some remarkable specializations (Immelmann, 1965). The suggestion that it is closely related to *modesta* (*Aidemosyne*) does not seem well substantiated.

Even though neither *Spermestes* nor *Euodice* is sufficiently different from *Lonchura* to justify generic separation, I have recognized them as subgenera for those who like to emphasize their distinctiveness.

The grouping and the sequence of species in *Lonchura* (*sensu stricto*) is a problem. Certain groups are well defined, for instance the *castaneothorax* group (with *flaviprymna, castaneothorax, teerinki, stygia, monticola, montana,* and *melaena*). Another fairly well defined assemblage consists of *punctulata, kelaarti, leucogastra, molucca, leucogastroides, fuscans,* and *striata.* The two New Guinea species *tristissima* and *leucosticta* stand well apart. The difficulties are with the remaining species. *L. quinticolor* (Lesser Sunda islands) is usually placed near *grandis* of New Guinea, but the similarity may well be superficial. The species *maja* and *pallida* are usually placed near the *castaneothorax* group, supposedly connected by *flaviprymna,* but I consider this similarity as secondary. *L. flaviprymna* seems to have lost the typical characters of the *castaneothorax* group, perhaps as a result of life in arid Australia. There has been a good deal of parallelism and convergence in this group of mannikins, and further analysis of songs and other characters is needed. (The sequence adopted in the Check-list attempts to bring close relatives together, but is surely not the last word.)

Amadina is perhaps the most aberrant genus of the mannikins. It does not quite fit with anything and is best listed last. Most likely it is an aberrant offshoot of the *Lonchura* group. *Padda* is close to *Lonchura,* but somewhat specialized. *Lonchura* is undoubtedly the central genus of this whole assemblage and the mannikins should be called Lonchurae.

It is possible that the three groups now informally designated as the Estrildae, Poephilae, and Lonchurae, will eventually deserve to be recognized as three tribes. At present, it seems however, that the differences are not sufficiently trenchant to justify tribal status.

Furthermore, there are too many genera, the placement of which is still doubtful. An informal classification, as first proposed by Delacour, would seem more appropriate for the time being.

REVISED SEQUENCE OF GENERA OF ESTRILDIDAE

I. ESTRILDAE

1 *Parmoptila*
2 *Nigrita*
3 *Nesocharis*
4 *Pytilia*
5 *Mandingoa*
6 *Cryptospiza*
7 *Pirenestes*
8 *Spermophaga*
9 *Clytospiza*
10 *Hypargos*
11 *Euschistospiza*
12 *Lagonosticta*
13 *Estrilda*
14 *Amandava*

II. POEPHILAE

15 *Aegintha*
16 *Emblema*
17 *Oreostruthus*
18 *Neochmia*
19 *Poephila*

III. LONCHURAE

20 *Erythrura*
21 *Chloebia*
22 *Aidemosyne*
23 *Lonchura*
24 *Padda*
25 *Amadina*

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THE EPIDERMAL GLANDS OF *LYGODACTYLUS* (GEKKONIDAE, LACERTILIA)

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Recent histological and ultrastructural studies have shown that the squamate epidermis is quite different from that of other vertebrates. In snakes and lizards, unique "epidermal generations" (Maderson, 1967) can be identified. These units, whose periodic appearance, maturation, and loss are reflected in a series of differing histological pictures at various times in the sloughing cycle, are made up of six (and sometimes more) different cell populations arising sequentially from an apparently homogeneous stratum germinativum. Some of these populations, e.g. those that form the superficial *Oberhautchen* component of the β-layer, or the innermost "clear layer," normally comprise only a single contiguous cell layer over the entire body surface. Others, e.g. the cells comprising the remainder of the β-layer, or the α-layer, are represented by numerous cell layers, although there may often be considerable variation from one genus or species to another or even from one part of the body or from one scale to another.

Although the details of the morphology of the squamate epidermis have only recently been reported (Maderson, 1965a, b, 1966b, 1967; Maderson and Licht, 1967; Roth and Jones, 1967), certain specialized modifications of this organ system have been described. Conclusive demonstration of an associated nerve supply (Miller and Kasahara, 1967) has confirmed the identity of so-called "sense organs" in lizards, described by earlier workers (Schmidt, 1920; Preiss, 1922). These studies, and those of the climbing organs of gekkonid and anoline lizards (Maderson, 1964a; 1966a; Ruibal and Ernst, 1965; Ernst and Ruibal, 1966; Lillywhite and Maderson, 1968) have shown that although the primary function of the *Oberhautchen* is to facilitate sloughing

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(Maderson, 1966b), this cell layer has undergone considerable adaptive specialization in various lizard groups.

Specialization of the squamate epidermis is not restricted to the formation of sensory and climbing organs; gland-like structures have also been reported (Cole, 1966a, b). While I was assembling material for a study on the so-called "glandular escutcheon scales" (Taylor and Leonard, 1956) of the Central American gekkonid *Gonatodes*, Dr. E. E. Williams of Harvard University drew my attention to the recorded presence of apparently similar structures in the East African gekkonid *Lygodactylus* (Pasteur, 1964). Preliminary examination of a few specimens revealed fundamental differences in the microscopic anatomy of the organs in the two genera. The structure of the escutcheon scales of *Gonatodes* proved to be not only of intrinsic interest but also contributed considerably to our understanding of the pattern of development of a squamate epidermal generation (Maderson, 1967). From a comparative cytological point of view, the superficially similar structures in *Lygodactylus* are more of a curiosity than of fundamental significance, but a detailed account of their structure is warranted for other reasons. First, it provides another example of the remarkable evolutionary potential of the squamate epidermis for the formation of specialized structures; second, it represents a further contribution to our knowledge of gekkonid anatomy; and finally, it helps to shed some light on the problem of the homology of the various types of "pores" found in gekkonids (Kluge, 1967).

MATERIAL AND METHODS

Through the courtesy of Dr. E. E. Williams of Harvard University and Dr. J. Peters of the Smithsonian Institution, I was able to obtain 29 male specimens of *Lygodactylus* spp. Loveridge's (1947) and Pasteur's (1964) statements to the effect that only males show the specialized glandular scales and pre-anal pores were confirmed by dissection and histological examination of 12 females from the same sources. The species were identified as *L. gutturalis, L. picturatus, L. p. keniensis* and *L. fischeri* from various known localities in East Africa. No significant differences in the structure of the glands were seen between species.

Pieces of skin were removed from the posterior abdominal surface just anterior to (but sometimes including) the pre-anal pores, or from the ventral aspect of the femoral region, which shows similarly modified scales (see below). Histological examination revealed that there are similarly modified scales between the line of

pre-anal pores and the vent, but there are no external indications of their presence. The history of some of the material was uncertain but it was probably fixed in the field in formalin and later stored in 70 per cent alcohol. The specimens were dehydrated in alcohol, cleared in chloroform, embedded in 56°C paraffin, and cut at 7μ vertical to the skin surface, either transverse or longitudinal to the scale axis (see below). Sections were mounted serially, a few from each ribbon being mounted unstained and examined by phase contrast. The remainder were stained in Ehrlich's hematoxylin and eosin, or aniline blue-orange G, or Masson's trichrome (Gurr, 1958). The material in the pre-anal pores proved to be exceptionally difficult to cut, giving confirmatory evidence of its nature (see below).

OBSERVATIONS

The Scales

Macroscopic appearance. The posterior abdominal, ventral femoral, and ventral tibio-fibular scalation is quite different in the males (Pl. 1, fig. 1, left) than in the females (Pl. 1, fig. 1, right). In the male, 2 to 3mm anterior to the vent, there is a transverse row of slightly enlarged scales on whose outer surface (Maderson, 1964b) is seen a circular opening about 0.3 mm across, in which a plug of material may be seen. There are 7 to 9 of these so-called "pre-anal" pores depending on the species (Pasteur, 1964); not infrequently there may be one or more which is considerably larger than the others. In the male, the darker pigmentation of these regions is distinctive. The scales lying in a blunt V-shaped area leading forwards from the line of pre-anal pores are the same shape (regularly trapezoid, the short axis lying parallel to the body axis, with little overlapping of successive elements) as the more anterior abdominal scales, but are distinctly darker. On the femoral region there are patches of scales of essentially similar shape (Loveridge, 1947), which are very much darker than those on the abdomen. This femoral patch grades into non-specialized, lighter-colored scales anteriorly (Pl. 1, fig. 1, left) but ends sharply posteriorly. There is a similarly modified patch on the ventral aspect of the tibio-fibular surface (Loveridge, 1947). The individual scales all show a more lightly pigmented marginal area; this is seen in histological sections to indicate the lateral margins of the specialized zones on each outer scale surface (Maderson, 1964b).

Microscopic appearance. As has been described elsewhere for *Gonatodes* (Maderson, 1967), the glandular scales of *Lygodactylus*

show a number of different histological conditions which can be interpreted as manifesting changes in association with periodic sloughing. This assumption will be followed in the descriptions below of four significantly different conditions which are important in interpreting the morphological structure of the specialized scales.

All the specimens examined showed conditions which could be interpreted as belonging to the "proliferation-renewal phase" (Maderson, 1965a, b, 1966b, 1967; Maderson and Licht, 1967). That a large museum sample should show 100 per cent of the material in the proliferative phase is very unusual in the author's experience. Mr. Allen Greer of Harvard University collected the 21 specimens examined of the Kenyan *L. picturatus* during an ecological study (Greer, 1967), and he provided me with further data regarding this material. The animals were caught by hand, or shot with dust-shot, and then fixed in formalin within at least four hours. Experience in collecting Australian gekkonids (Maderson, unpublished data) suggests that the stress of capture initiates a new epidermal cycle (Maderson, 1967), with the result that material obtained from animals kept in captivity for three or four days will always show various stages in epidermal proliferation. Although Mr. Greer tells me that he rarely saw *L. picturatus* actually sloughing, on the few occasions that he did so, they were engaged in removing material from their body surfaces with their teeth. This behavior pattern has been described in a number of squamate species (Bustard and Maderson, 1965). In *Gekko gecko* (Chiu, Phillips and Maderson, 1967) and *Anolis carolinensis* (Maderson and Licht, 1967) the complete physical removal from the body of the material to be shed is accomplished in a very short time (something less than 5 hours and often during the night [Maderson, unpublished data]). Although the material examined here did not permit an estimate of the time occupied by the various stages of epidermal differentiation (Maderson and Licht, 1967), the picture which emerges is that *Lygodactylus* either sheds very frequently or else has a cycle in which the "resting phase" (Maderson, 1967) is extremely short or absent. It would be of interest to know to what extent this is associated with the probable ecological and behavioral significance of the glands and pores (Cole, 1966a, b).

In median longitudinal section the individual scales are seen as triangular structures arising from the body surface with very little overlapping of adjacent elements (Pl. 5, fig. 2). In transverse section the picture varies depending on the level along the scale axis, but in general one sees a rather wide-based structure, again with little overlap of adjacent scales. The outer scale surface (Maderson, 1964b) is always distinctly concave with the deepest portion

towards the posterior distal region of the scale; it is in this concavity that the specialized epidermal material is seen. In gross and low-power microscopic appearance there is a very general similarity to the escutcheon scales of *Gonatodes* (Maderson, 1967).

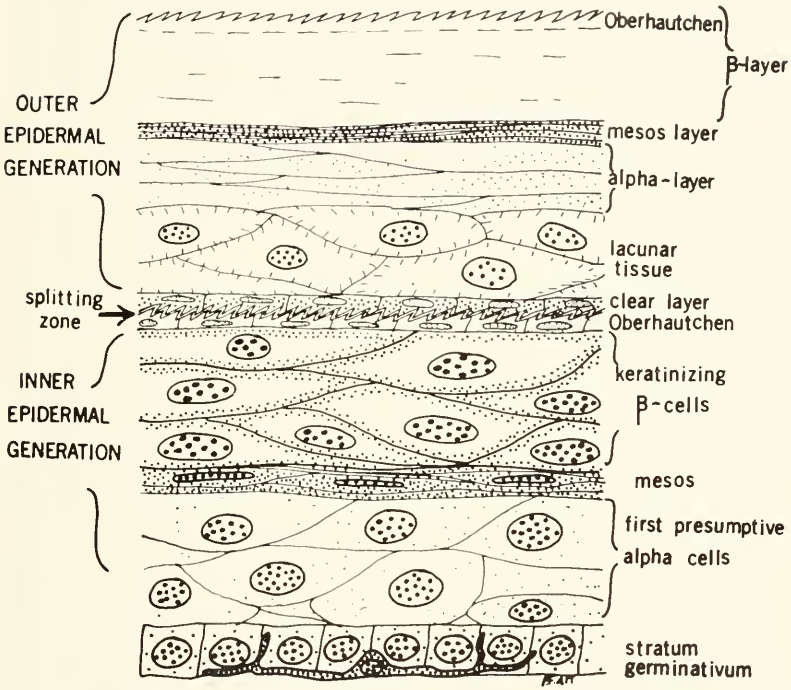

Figure 1. Schematic representation of a generalized squamate epidermis several days before sloughing is due to take place. (Figure taken from Maderson [1967] and reproduced here by kind permission of the editors of Copeia.)

To avoid undue repetition of references in the text of the following descriptions, all the terms used are those discussed and defined in previous works (Maderson, 1965a, 1966b, 1967; Maderson and Licht, 1967). This nomenclature is shown in schematic form in Figure 1.

Condition One (6 specimens); Pl. 1, figs. 2-4.

Plate 1, figure 2 shows a sagittal section through a scale taken from the anterior margin of the specialized abdominal region where the gland development is smallest; an enlarged portion of the low-power view is shown in Plate 2, figure 4.

The surface of the body is formed from a homogeneous, chromophobic tissue which shows no indications of nuclear remains or cell outlines; this is the β-layer of the outer epidermal generation. The extreme superficial surface of the β-layer is formed by the characteristic *Oberhautchen* which in gekkonids (Maderson, 1966b, 1967; Ruibal and Ernst, 1965) is always seen as a series of minute vertical spinules (Pl. 1, fig. 4). Towards the distal portion of the outer scale surface, the *Oberhautchen* is separated from the normal β-material described above by a quite different material (Pl. 1, fig. 4). The latter is basophilic in hematoxylin stained sections and stains a patchy orange and blue in sections stained with aniline blue/orange G. This suggests that the material is of a keratinaceous nature, as adjudged by its affinity for orange G (Gurr, 1958), but with a mixed complement of possible mucoprotein material which stains with the aniline blue. There are also copious deposits of melanin granules. This is here termed the β-gland material, for reasons which will be discussed later. Initial examination posed the problem of how this could be regarded as a "gland" if the material was confined between the *Oberhautchen* (which is a very strong unit in spite of its being composed of only a single cell layer [Maderson, 1966a]) and the rest of the β-layer. Although examination of serial sections showed that often only the edges of the material, proximally, distally, and laterally were covered by the *Oberhautchen*, it was assumed that histological preparation had destroyed a contiguous central portion. The proof that this is not so will be presented later, and in fact there is an approximately circular area on the outer scale surface where the gland material is directly exposed to the external environment; this is due to a regional non-development of the *Oberhautchen*. This is the first time that the author has ever seen a situation where there is not a continuous *Oberhautchen* over the whole epidermis so as to cover the entire body surface. Even on the inner scale surface and in the hinge region where the β-layer is often difficult to recognize histologically, ultrastructural studies (Ernst and Ruibal, 1966) have shown that the β-layer is represented here by the *Oberhautchen* alone.

The β-layer invariably separates from the underlying tissues during histological preparation, and the artifactual gap is traversed by refractive strands which represent the only histological indications of the mature mesos layer. This is often difficult to identify in geckos but is marked by an X in Plate 1, figure 4.

Beneath the mesos layer is a region of lamellar chromophilic material containing dense deposits of melanin, showing no indications

of nuclei except for the occasional pycnotic figure seen as a presumptive α-cell becomes incorporated into the tissue (Maderson and Licht, 1967) at its very base: this is the α-layer of previous accounts. No further changes occur in the histological appearance of the tissues described thus far and they will not be mentioned again in subsequent descriptions.

Beneath the α-layer are two or more rows of flattened or rectangular cells. The outermost layer(s) (*plto*, Pl. 1, fig. 4) are not continuous over the entire outer surface of the scale where new gland material is seen (see below) but are easily recognizable in other regions (see below). This represents the presumptive lacunar tissue which plays an important role in the maturation of an epidermal generation prior to shedding (Maderson, 1967; Maderson and Licht, 1967). The innermost layer (*pclo*, Pl. 1, fig. 4) is not readily recognizable as a typical gekkonid clear layer (Maderson, 1966b, 1967) at this time, and only its later development really reveals its identity (see below). The tissues and layers thus far described comprise a "complete" outer epidermal generation (Maderson, 1967).

Between the presumptive clear layer and the stratum germinativum is a cell mass comprising tight-packed polygonal cells. In sagittal section (Pl. 1, fig. 4) there is a slight indication of oblique orientation of the cells towards the scale apex, but in transverse section (Pl. 1, fig. 3) their orientation is vertical away from the stratum germinativum. The nuclei are rounded in the early stages of development (Pl. 1, fig. 4) but tend to become ovoid later (Pl. 1, fig. 3). The cytoplasm presents a slightly filamentous appearance but is often floccular in the early stages of development. There is only a single recognizable cell type in the region at this time. This mass of cells represents the first indications of the new gland material which will eventually be exposed to the external environment after the next slough. As the number of cells in this region increases, the basally situated epidermal melanocytes extend dendrites far above the stratum germinativum and deposit melanin granules into the cells (Pl. 1, fig. 3).

The stratum germinativum consists of cuboidal cells when the cell mass above it first appears (Pl. 1, fig. 4), but there is a gradual change to a more columnar condition later (Pl. 1, fig. 3).

Condition Two (8 specimens); Pl. 2, figs. 1-2.

A longitudinal section of a major glandular scale (Pl. 2, fig. 1) shows that the most significant change from the previous condition is that the new gland material is now seen to be an integral cell mass confined distally by a region of highly flattened

cells and proximally by the stratum germinativum. The flattened cells (Pl. 2, fig. 1) beneath the darkly chromophilic α-layer will eventually form a 2 to 3 layered lacunar tissue, which will be bounded basally by a clear layer, and the flattened layer beneath this (the one forming the outermost boundary of the mass of new gland material cells) will become the *Oberhautchen*. Two points must be emphasized here. First, the cell layers which are here termed the "presumptive clear layer" (*pclo*, Pl. 2, fig. 2) and the "presumptive *Oberhautchen*" (*pObi*, Pl. 2, fig. 2) are not yet recognizable on the basis of their cytology, only by their topographical position. Second, Plate 2, figure 2 shows a section through a lateral part of a scale where a distinct lacunar tissue and clear layer/*Oberhautchen* complex forms (see below); the picture in a median sagittal plane would be very different. Here the base of the mature α-layer would lie directly against the uppermost cells of the mass of new gland material. The high power micrograph of the lateral margin as seen in transverse section (shown as Pl. 2, fig. 2) shows some of the cytological detail visible at this time. In this particular field the lacunar tissue is not developed (it is of variable occurrence and distribution in lacertilians [Maderson, 1966b; Maderson and Licht, 1967]). The *Oberhautchen* (which is not as regular in shape here as over the general body surface of other gekkonids [Maderson, 1966b]) is just recognizable under oil immersion by the slightly thickened outermost cell membranes. The overlying clear layer is also distorted in most regions of the glandular scales in *Lygodactylus*, as compared with that of other gekkonids (Maderson, 1966b).

The extraordinary variations in cell shape, distribution of elements, etc., described above would make identification of the lacunar tissue, clear layer, and *Oberhautchen* very tenuous, were it not for the fact that in serial sections the various regions and layers can be traced along the adjacent "semi-specialized" (see later) and unspecialized scales. In these last locations, the histology approaches the conditions described for the normal body epidermis of *Gekko gecko* during the early proliferative phase (Stages 2 and 3 [Maderson, 1966b]). Certain features of these adjacent regions, which provide clues as to the homologies of the various cell types seen in the specialized scales of *Lygodactylus*, will be discussed later.

Condition Three (13 specimens); Pl. 2, figs. 3, 4; Pl. 3, figs. 1, 2.

In these specimens one sees the laying down and subsequent maturation, i.e. keratinization, of cells which can be recognized as

a β-, a mesos, and a partially formed α-layer of the inner epidermal generation (Maderson, 1967). The pattern of histological changes occurring in the lacunar tissue and clear layer of the outer epidermal generation supports the general assumption that the gland scales resemble a much-modified form of the typical gekkonid body epidermis during the pre-sloughing period (Stages 3-5 [Maderson, 1966b]). Apart from the gland material, all of the regions which are identified and discussed below are contiguous with similar regions of the epidermal surface of adjacent unmodified scales which resemble exactly the general body epidermis described elsewhere (Maderson, 1966b).

A low-power view of a transverse section through a glandular scale when the first presumptive β-cells become visible is shown in Plate 2, figure 3, and the region indicated by the vertical strip is shown in Plate 3, figure 1. The latter shows a portion of the scale where the new gland material is not bounded by an *Oberhautchen* and there is no clear layer or lacunar tissue associated with the outer epidermal generation, so that the outermost layer of new gland cells abuts directly onto the base of the α-layer, which is shown artifactually split away in Plate 2, figure 3.

The mass of cells termed the "new gland material" (Pl. 2, fig. 3) shows two distinct types of cell. The most predominant form is a polygonal shaped cell with a slightly thickened membrane and relatively large central ovoid or rounded nucleus lying in a densely filamentous cytoplasm (Pl. 3, fig. 1). These filaments are slightly basophilic in hematoxylin stained sections and also show a strong affinity for orange G. The only similar cytological picture which the author has ever seen is in chick scales during the later embryonic stages when the characteristic avian β-keratin is being laid down in that location (Baden and Maderson, unpublished data). For this reason and to distinguish the glands of *Lygodactylus* from the escutcheon scales of *Gonatodes* (the formative stages of which are *totally* different [Maderson, 1967]), I suggest that these abdominal glands in *Lygodactylus* should be termed "β-glands." In a series of specimens I have observed the gradual death of these cells, as indicated by the increasing frequency of pycnotic figures (Pl. 3, fig. 2; Pl. 4, fig. 3). The filaments become less and less distinct and the entire cell eventually becomes either finely basophilic (hematoxylin) or totally orange in orange G-stained material. The conspicuous thickening of the cell membranes which normally (Maderson, 1966b, 1967) characterizes the cytogenesis of the subjacent presumptive β-cells is not seen here; this may be due to

the fact that the gland material never becomes quite as homogeneous in appearance in its mature state as does the actual β-layer of the outer epidermal generation (see p. 6).

The second cell type seen in the mass of presumptive gland material has a quite different cytology. In hematoxylin and eosin sections the cytoplasm is floccular and is faintly eosinophilic. The central nucleus is about the same size and shape as that of the other cells. In sections stained with aniline blue the floccular appearance takes on the form of a dense blue mesh-work with occasional deep-staining blue granules. These cells are scattered randomly between the filament-filled cells in the main body of the new gland material (Pl. 3, fig. 1; *X*) but tend to be concentrated in clumps around the lateral, proximal, and distal margins of the material (Pl. 3, fig. 3; Pl. 4, fig. 2; *X*). These positions correspond to portions of the mature material where the blue-staining (with aniline blue/orange G stain) is most dense. On adjacent scales (Pl. 4, fig. 1), cells of a similar nature are seen, but their distribution and relative abundance are different. Here a distinct *Oberhautchen* with characteristic spinules is seen; beneath this are 1 to 3 layers of the blue-staining granular cells (Pl. 4, fig. 1; *gc*), and beneath these, in turn, normal presumptive β-cells in various stages of maturation are seen. In other instances (further away from the main "gland area" on the abdominal and limb surfaces) occasional cells of this type are seen. In the latter, the cytoplasm resembles that of the "protruding" *Oberhautchen* cells seen in the epidermis of *Gekko gecko* (Maderson, 1966b, p. 43), except that whereas the latter definitely showed spinules on the outer membrane, in *Lygodactylus* the cells contact the clear layer cells directly with no indication of spinule development. A final point which will be of significance in homologizing the various cell types is the fact that in *Lygodactylus* (and numerous other gekkonid species [Maderson, unpublished data]) *definite Oberhautchen* cells, i.e. cells which eventually form the outermost surface of the body, which develop in association with overlying clear layer cells, and which show various degrees of spinule development, can be seen to contain granules which stain with aniline blue; these granules are not seen in the underlying presumptive β-cells.

Material showing this condition confirms the regional absence of the *Oberhautchen* covering over much of the gland material; the very sharp discontinuity of this covering is seen in transverse (Pl. 3, fig. 2) and sagittal (Pl. 3, fig. 3) sections (see arrows). The clear layer and lacunar tissue are also absent from those regions where there is no *Oberhautchen*. A slight problem is presented by

the morphology of the cell layer indicated by *Y* in Plate 3, figure 3. This layer lies between the main mass of new gland cells and the easily recognizable presumptive β-cells which are nearly fully keratinized. Plate 3, figure 3 shows that this cell layer is very different from the underlying cells and does not contain the conspicuous filaments seen in the gland cells. In many ways it resembles a typical gekkonid *Oberhautchen* except for a complete absence of any sign of spinule development. However, the total lack of any indication of topographic continuity between this layer and the *Oberhautchen* (of characteristic gekkonid form) finishing at the arrow (Pl. 3, fig. 3) suggests that the cytological similarity is misleading. I suggest that there is a large area where there is no development of a characteristic *Oberhautchen;* this point is important in assessing the homologies of the various cellular elements in the glandular scales.

The morphological appearance and subsequent maturation of the cell layers termed the lacunar tissue and the clear layer are exactly the same as those described in *Gekko gecko* (Maderson, 1966b, 1967). Subsequent development of the elements comprising the rest of the inner epidermal generation (presumptive β-cells, presumptive mesos layer, presumptive α-cells) is also quite typical, and details of their structure will be found elsewhere (Maderson, 1966b, 1967; Maderson and Licht, 1967). The columnar appearance and relative chromophobia of the stratum germinativum cells as the mesos layer is laid down (Pl. 4, figs. 1, 2, 4) (Maderson and Licht, 1967) are emphasized.

Condition Four (2 specimens); Pl. 2, fig. 5; Pl. 4, fig. 4; Pl. 5, fig. 1.

One specimen showed a very late phase in the keratinization of the new β-layer of the inner epidermal generation, with subjacent presumptive mesos cells showing pycnotic figures, and beneath these numerous presumptive α-cells (Maderson, 1966b, 1967; Maderson and Licht, 1967). Another (Pl. 5, fig. 1) showed a definite "pre-sloughing" condition with the inner epidermal generation having a mature β-layer, a mature mesos layer showing as refractive strands, as described earlier, and with the first indications of a new α-layer beneath. Beneath the 3 to 4 layers of presumptive α-cells which would normally be incorporated into the α-layer during the post-sloughing period (Maderson, 1966b, 1967; Maderson and Licht, 1967), there were some cells which resembled exactly the first indications of the next mass of new gland cells, as described earlier. In the absence of more material one hesitates

to make definitive statements, but it is probable that this genus never shows a typical "resting phase" in the sloughing cycle.

Sloughing, i.e. the physical removal of the outer epidermal generation from the body surface, involves the separation of the clear layer of the outer generation from the *Oberhautchen* of the inner generation (cf. Fig. 1; Maderson, 1966b, 1967; Maderson and Licht, 1967) as seen in Plate 5, figure 1, left. Where the clear layer/*Oberhautchen* complex is absent (over the central portion of the new gland material), the separation occurs at the base of the old α-layer, which lies directly on top of the new gland material (Pl. 5, fig. 1, right). Cell shapes are still visible in the latter at this time, and the material appears to occupy a greater vertical depth than does the mature material; this may be due to drying of the material once it is exposed to the external environment. The staining characteristics of the gland material in the pre-slough specimen are exactly those of the exposed material (see p. 6).

The Pre-anal Pores

Macroscopic appearance. The external appearance of the pore openings has already been described above (p. 3). Dissection of the integument in the pre-cloacal region reveals the inner portions of the pores as apparently simple sacs running directly anteriad from the opening for a distance of 1.2 to 1.4 mm. The sacs lie between the subcutaneous tissue and the ventral musculature. They are surrounded by fat.

Microscopic appearance (Pl. 5, figs. 2-4; Pl. 6, figs. 1-4). A median longitudinal section through the opening of a pre-anal pore is shown in low power view in Plate 5, figure 2. The scales anterior and posterior to the scale on which the pore opening is situated show β-glands in "condition three" as described above. It is noteworthy that the rest of the epidermis on either side of the pore lumen is not modified in any way (Pl. 5, figs. 3 and 4) and its structure is that which has been described elsewhere (Maderson, 1966b) as a stage four condition of the normal gekkonid body epidermis. Plate 5, figure 4 gives a clear picture of the slightly modified condition normally seen towards the inner scale surface and hinge region where there is quite extensive development of a lacunar tissue (*lto*) in which the characteristic basophilic granules (keratohyalin? [see discussion, Maderson, 1966b]) are to be seen. Following the epidermis from the scale surface into the mouth of the pre-anal pore, one sees the striking discontinuity of all the component layers and regions seen on the normal epidermis; these

are marked by arrows in Plate 5, figures 3 and 4. The most rigorous examination of the pre-anal pore walls (see below) reveals no homologous layers or any resemblance to them, except for a stratum germinativum. The major portion of the mouth of the pre-anal pore in Plate 5, figure 2 is empty, but numerous fragments of the original "plug" of material can be seen. This material is very much harder to cut than either the β-gland material, the escutcheon gland material of *Gonatodes* (Maderson, 1967a), or iguanid gland material (Maderson, unpublished data). It is very slightly eosinophilic and stains fairly densely with orange G. The shape of the individual fragments suggests that they are single, hardened cells, but there are no signs of nuclear remains in the mature material. The histological structure of the lining and of the lumen contents varies as one follows down the length of the gland.

At about the region where the gland turns rather sharply forward (Pl. 5, fig. 2), the lumen is normally filled with mature material as described above and the lining shows the histological picture seen in Plate 6, figure 1. There is a cuboidal stratum germinativum and above it 2 to 3 layers of loosely arranged, slightly flattened cells. There is no indication that new cells, contributing to the actual pore material, arise from this region.

About half-way down the length of the pore, immature glandular material may be seen (Pl. 6, fig. 2). This stains deeply with orange G, individual cells can be recognized, and some contain pycnotic nuclei. There is no obvious separation between these cells and the mature material described above; they merge imperceptibly into one another.

In the anterior portion of the gland the histological picture is quite different. Just beyond the region described above there are masses of tightly packed cells of irregular polygonal shape with a strongly heterogeneous fibrillar cytoplasm (Pl. 6, fig. 3). The nuclei are all viable and the cytoplasm appears to contain tightly packed fibrillar elements lying in an effectively floccular matrix. The fibrils stain intensely with orange G, suggesting a keratinaceous nature, while the background is patchy blue, indicating an uptake of aniline blue. There is no indication of thickening of the cell membranes. The figure suggests that intercellular spaces are common; this is an artifact of sectioning, since certain regions show this appearance, but in other parts the cells are closely packed.

At the base of the pore are seen cells which can reasonably be interpreted as "mother cells." Their very specific appearance gives a clear indication of how the cells described above are formed. Lines of columnar cells reach into the pore lumen from the stratum

germinativum. Those nearest the germinal layer (Pl. 6, fig. 4) show a distinct division into three parts. Nearest the germinal cells, the relatively large, ovoid nucleus can be seen. Next, there is a region of cytoplasm with a slightly amorphous appearance, sometimes suggesting irregular droplets or granules; this region stains conspicuously with orange G. The distal portion of the cell contains a large droplet (Pl. 6, fig. 4; arrow); this is slightly eosinophilic but stains particularly intensely with aniline blue. As the cells move out into the lumen, and begin to move towards the pore mouth, the orientation of the three portions is lost, and the distinct droplet soon disappears. One assumes that the patchy blue staining visible in cells further up the lumen results from a disintegration of the large droplets and a spreading of the material throughout the cell cytoplasm.

All the various stages described above were visible at various levels wherever a portion of pre-anal gland material had been sampled with the overlying scales; there was no indication of any cycle of activity.

DISCUSSION

There have been comparatively few studies of specialized "glandular structures" in lizards (Cole, 1966b), and those works which are available are for the most part concerned with follicular glands, such as femoral pores (Cole, 1966a).

Taylor and Leonard (1956) considered the "escutcheon scales" of *Gonatodes*, and I have recently re-examined the problem in the light of our present knowledge of the squamate epidermis (Maderson, 1967). The specialized scales of *Gonatodes* and of *Lygodactylus* are similar in that their pattern of formation is intimately associated with the periodic sloughing cycle of the epidermis, but here the similarity ends.

The major differences between the mature and developing gland material in the two genera can best be expressed in the following table:

Gonatodes (Maderson, 1967)	*Lygodactylus*
1. Specialized scales restricted to a V-shape anterior to cloaca. (N. B. In other sphaerodactyline forms [*Sphaerodactylus*, Thomas and Schwartz, 1966] specialized scales may be found on the femoral region also.)	1. Specialized scales seen on posterior abdomen, immediately anterior to the cloaca, and on the ventral aspects of the hind limbs.

2. Gland material is borne on the surface of the β-layer of the outer epidemal generation and has an incomplete *Oberhautchen* running *beneath* it.	2. Gland material is found *in* the β-layer of outer epidermal generation with an incomplete *Oberhautchen* partially covering it.
3. Gland material is derived from the *basal* portion of the epidermal generation which was lost at the previous slough. Thus in the "resting phase" there are tissues in the epidermis derived from two *different* epidermal generations.	3. Gland material is derived from the *superficial* portions of the epidermal generation upon which it is borne. As there is some doubt that a true "resting phase" ever exists, there may always be tissues from two different generations present in the epidermis, but for quite different reasons (see text, p. 11).
4. Single cell type seen in developing gland material.	4. Two distinct cell types seen in developing gland material.
5. Staining of keratinaceous elements of the gland material suggests an affinity with the α-layer	5. Staining of keratinaceous elements of gland material suggests an affinity with the β-layer.
6. At sloughing, splitting zone over glandular material is at base of the ∝-layer of the outer epidermal generation, leaving a portion of the outer epidermal generation behind.	6. At sloughing, entire outer epidermal generation is lost. Although the splitting zone does occur at the base of the α-layer of the outer generation over the gland material, this is due to a partial non-development of the lacunar tissue and clear layer of the outer generation.

These differences are so fundamental that I suggest the specialized scales in the two genera are not in any way homologous.

The problem of the relationship of the specialized scales to the pre-anal pores is slightly complicated by the possibility that this particular genus has no true resting phase in its sloughing cycle. Cole (1966a) suggests that there is a continuation of the normal epidermis (referred to in his paper, pp. 125-126, as the "stratum corneum") into the femoral gland mouth in *Crotaphytus*, which splits the "plug" into an outer portion which is lost at shedding and an inner portion which takes the place of the latter. This would imply that glandular activity is directly correlated with the epidermal sloughing cycle. Cole (1966a) also suggests that there is some evidence that there is annual cyclical activity of the iguanid femoral

pores. In a study of *Gonatodes* (Maderson, 1967), I have indicated that gekkonids typically shed very frequently throughout the year. *If* there is indeed *annual* cyclical activity of the gland (? in association with the reproductive cycle), then one would have expected that at some stage in the evolution of true pores or glands, their pattern of cyclical protein synthesis would have had to become *independent* of the rest of the epidermis. In *Gonatodes* (Maderson, 1967) there are morphological indications of how this might have occurred. As far as one can tell in *Lygodactylus* there is no indication of a separation between the completely mature pre-anal pore material and the cells still undergoing differentiation, so that the pre-anal pores in this genus resemble a tube of tooth-paste from which material is slowly squeezed out. It is unprofitable to speculate on this point in the absence of material collected throughout the year in an attempt to demonstrate a true annual cycle of activity in the pre-anal pores.

Apart from the problem of the relative activity of the pre-anal pores and the β-glands, there is the problem of the relationship between the two types of structure. Here I would unhesitatingly suggest that the β-glands represent an ancestral condition of the pre-anal pores *in this genus* (see below). The striking discontinuity of the *Oberhautchen* has been emphasized. If, in association with gland development on the scales, one can see the absence of a superficial layer, there is no logical reason to deny the possibility that subjacent layers could also be reduced and eventually lost during evolution. In fact I have demonstrated that this process has already begun in the absence of the lacunar tissue and clear layer from the central portion of the β-glands. Thus, reference to Plate 5, figure 2 shows that one only has to imagine that the rest of the epidermal generation beneath the developing gland material (presumptive-β-cells, presumptive mesos cells and presumptive α-cells) could disappear and one would be left with a "shallow pre-anal pore." Furthermore, the figure shows that if a particular portion of the individual scale, i.e. the portion over which the gland material forms, invaginated deeper and deeper into the subcutaneous tissues, a pre-anal pore type of structure would be developed. The epidermis of the scale upon which the pore opens is notably different from the adjacent scales showing no indication of normal gland development; this would be homologous with the extreme unmodified margins of the β-gland scales which show a quite typical "normal body epidermis" structure (Maderson, 1966b). A consideration of probable intergeneric homologies of scales and pores

depends on the interpretation of the various component cell types which will be discussed next.

The presence of two distinct cell types in the β-glands has been emphasized. Although the chemistry of epidermal proteins is a highly complex field, and consideration thereof is not pertinent to an article of this kind, it is permissible to suggest that those cells which show a definite affinity for orange G are synthesizing a keratin, while those showing an affinity for aniline blue are synthesizing a mucoprotein of some description. The vertebrate epidermis has the capacity to form either keratins or mucins, as evidenced by studies on the structure of the amphibian epidermis (Parakkal and Matoltsy, 1964), and under certain experimental conditions (New, 1963). It seems that in *Lygodactylus* β-glands the two functions are carried on within different cells. However, there is evidence from adjacent scales in this and other genera which suggests that *Oberhautchen* cells (or at least, cells belonging to the same portion of the epidermal generation as the *Oberhautchen* or presumptive β-cells) are capable of both activities. Whether these modified cells occurring either singly or in a double or triple epithelium (Pl. 4, fig. 1) should be regarded as "*Oberhautchen*" cells is a semantic problem; one would prefer to retain the term only for those cells which show the characteristic development of spinules or setae on the outermost membrane (Ruibal and Ernst, 1965; Ernst and Ruibal, 1966). Within the pre-anal pores, there is no indication of two distinct cell types. There is however evidence of localization of mucoprotein synthesis and keratin synthesis within a single cell. This then should be regarded as a specific specialization of the tendency seen in *Oberhautchen* cells on the non-specialized scales of this and other genera. In the femoral pores of *Gekko gecko* (Maderson, unpublished data) such "mixed-function" cells are not seen; here there are cells which only stain positively for keratin and cells which only stain positively for mucoprotein. A "non-association" with normal epidermal proliferation is also seen in *Gekko gecko,* as indicated by the discontinuity of all the normal layers and regions of the inner epidermal generation at the femoral pore mouth, exactly as has been described here in *Lygodactylus*. Although there is a need for detailed studies of the basic anatomy and possible cyclical activity in glands from a variety of gekkonid types, it is suggested that the problem of direct homology between the pre-anal pores of *Lygodactylus* and the femoral pores of *Gekko gecko* will be one of semantics. Granted that there are situations where "single-function" and "mixed-function" cells may be identified, the fundamental relationship of the

pore cells to the normal epidermal generation is more important. Thus I suggest that there is some evidence that lygodactyline β-glands are definitely homologous with the pre-anal pores of that genus and with the femoral pores of *Gekko gecko* — all materials deriving from the outermost portions of the epidermal generation — but there is no evidence of homology with the type of glandular scale seen in the sphaerodactyline gekkonids, where the glandular material derives from the innermost portions of an epidermal generation. The absence of pre-anal pores from sphaerodactylines (Kluge, 1967) makes it impossible to prove or disprove Kluge's (1967) statement that the escutcheon scales in these forms are "almost certainly modified pre-anal organs" (p. 18). Taylor and Leonard (1956) suggested that the escutcheon scales of sphaerodactylines represented structures from which pre-anal organs in other groups were derived; the analysis of the cellular components in *Gonatodes* (Maderson, 1967) and the evidence presented here suggest that this is unlikely. In the present state of knowledge one can only surmise that the specialized scales thus far described in sphaerodactylines appear to be the result of an independent evolutionary pathway from those found in *Lygodactylus* and *Gekko gecko*. Further comment on the phylogenetic implications of scale, pore, and gland structure must await detailed analysis of material from a variety of forms.

SUMMARY

1. The histological structure of the scalation of the abdominal, femoral and tibio-fibular surfaces and pre-anal pores of 29 male specimens of *Lygodactylus* spp. has been studied.

2. The epidermis of the scales in these regions shows a number of histological conditions which can be interpreted as representing different stages in the histogenesis of the integument in association with periodic sloughing. All the characteristic elements of a typical squamate "epidermal generation" are represented. There is present an additional region consisting of a keratinaceous material with a mucoprotein component; this material develops in association with the β-layer of the epidermal generation and lies between the *Oberhautchen* and the subjacent β-layer. In the mature state the material is partially exposed to the external environment by a unique regional non-development of the *Oberhautchen*.

3. The pre-anal pores are simple invaginations of single scales running forwards in the ventral body wall musculature. There is no obvious indication of any cyclical activity, and it would appear that

the activity of these glands is quite independent of the sloughing cycle of the rest of the body covering.

4. Comparison of the structure and development of the modified scales with what is known of superficially similar "escutcheon scales" in sphaerodactyline gekkonids suggests that the two organ systems are of quite independent evolutionary origin, there being no evidence of any homology between them. To prevent further confusion in this context, it is suggested that the organs described here in *Lygodactylus* should henceforth be termed "β-glands."

5. Comparison of the structure of the β-glands with the pre-anal pores suggests that the former present a definite possible ancestral form of the latter *in this genus.*

6. The problem of the evolutionary relationships of gekkonid glands and pores is briefly discussed. The small amount of available evidence suggests the possibility that whereas there is a broad basis for assuming an homology between the pre-anal pores in *Lygodactylus* and *Gekko gecko,* no homology of any description can be assumed with the escutcheon scales of sphaerodactylines. The basis for assessing homologies of these epidermal structures in gekkonid lizards should depend on a consideration of the fundamental relationship of the "gland" material to the epidermal generation.

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ABBREVIATIONS USED IN PLATES

βi	β-layer of inner epidermal generation
βo	β-layer of outer epidermal generation
αo	α-layer of outer epidermal generation
clo	Clear layer of outer epidermal generation
clo/Obi	Clear layer/*Oberhautchen* complex
f	Filaments
gc	Granular cells
GM	Exposed glandular material
H	Hinge region
ISS	Inner scale surface
lto	Lacunar tissue of outer epidermal generation
m	Melanin granules
mi	Mesos layer of inner epidermal generation
mo	Mesos layer of outer epidermal generation
NGM	New glandular material
Obi	*Oberhautchen* of inner epidermal generation
Obo	*Oberhautchen* of outer epidermal generation
OSS	Outer scale surface
pβi	Presumptive β-layer of inner epidermal generation
pαi	Presumptive α-layer of inner epidermal generation
pclo	Presumptive clear layer of outer epidermal generation
plto	Presumptive lacunar tissue of outer epidermal generation
pmi	Presumptive mesos layer of inner epidermal generation
pObi	Presumptive *Oberhautchen* of inner epidermal generation
sg	Stratum germinativum

PLATES

PLATE 1

Figure 1. Posterior abdominal and sub-caudal surfaces of *Lygodactylus picturatus* male (left) and female (right). Note the darker scales on the abdominal, femoral and tibio-fibular surfaces of the male as compared with the female. The small square of tissue missing from the abdominal surface of the male is seen in figs. 2-4. Scale divisions in mm.

Figure 2. Low-power view of sagittal section through two successive scales from the region shown in fig. 1. The portion outlined is shown in fig. 4. This specimen shows the simplest form of "Condition One" (text pages 5-7). Hematoxylin and eosin stain.

Figure 3. High-power view of transverse section through a more typical "β-gland" from the abdominal surface showing a later "Condition One" than in figs. 2 and 4. The β-layer and the exposed gland material are absent. Hematoxylin and eosin stain.

Figure 4. Oil immersion montage of region outlined in fig. 2.

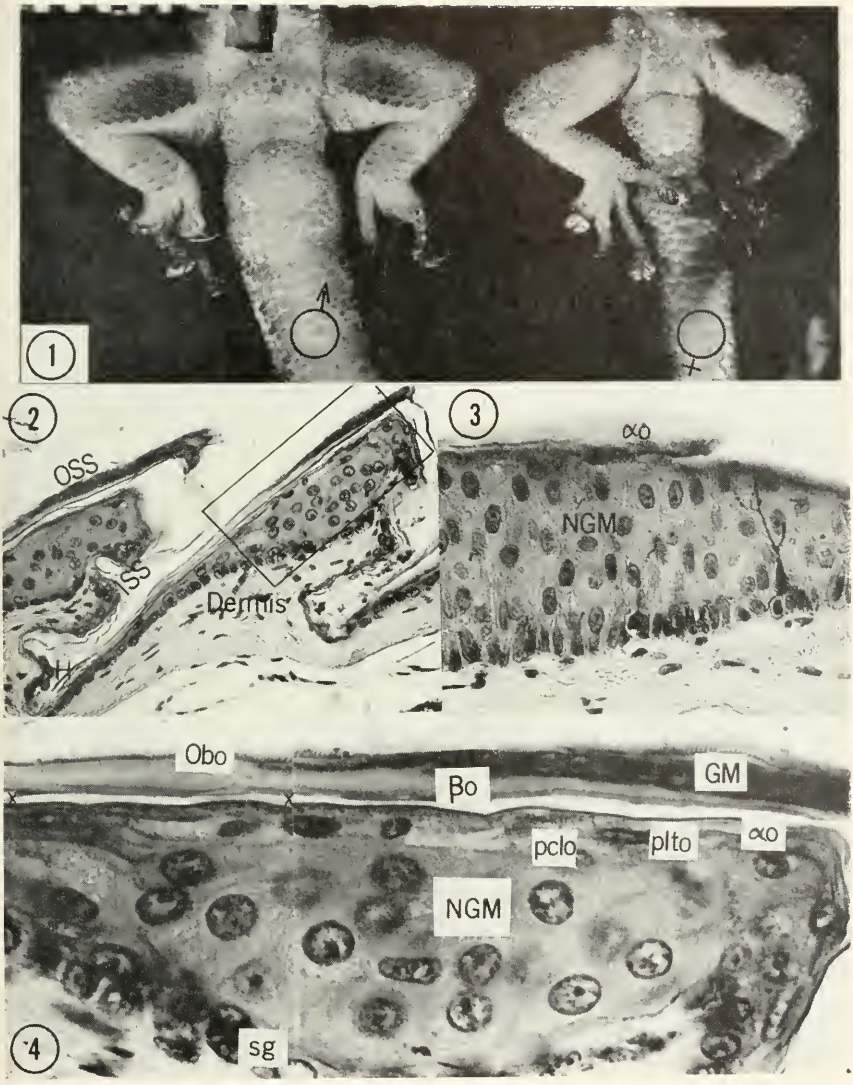

PLATE 1

PLATE 2

Figure 1. Sagittal section through epidermis of a specialized scale from the femoral region showing "Condition Two." Masson's trichrome stain.

Figure 2. Extreme lateral margin of a specialized scale from the femoral region showing "Condition Two" as seen in transverse section. This shows the layers of cells which will later be recognizable as the lacunar tissue, the clear layer and the *Oberhautchen*. The β-layer of the outer epidermal generation (represented only by the *Oberhautchen* in this region [Ernst and Ruibal, 1966]) is not shown. Hematoxylin and eosin stain.

Figure 3. Transverse section through a specialized scale from the abdominal surface showing an early "Condition Three." The β-layer of the outer epidermal generation and the exposed gland material are not shown. The region enclosed by the rectangle is shown in Pl. 3, fig. 1. Hematoxylin and eosin stain.

Figure 4. Transverse section through a specialized scale from the abdominal surface showing a mid-late "Condition Three." The β-layer of the outer epidermal generation is not shown. The region enclosed by rectangle marked *X* is shown in Pl. 3, fig. 2, and that marked *Z* is shown in Pl. 4, fig. 3. Aniline blue-orange G stain.

Figure 5. Median sagittal section through a specialized scale from the abdominal surface showing a very late "Condition Three" or early "Condition Four." The β-layer of the outer epidermal generation is not shown. A region comparable to that enclosed by the rectangle is show in Pl. 3, fig. 3. Aniline blue-orange G stain.

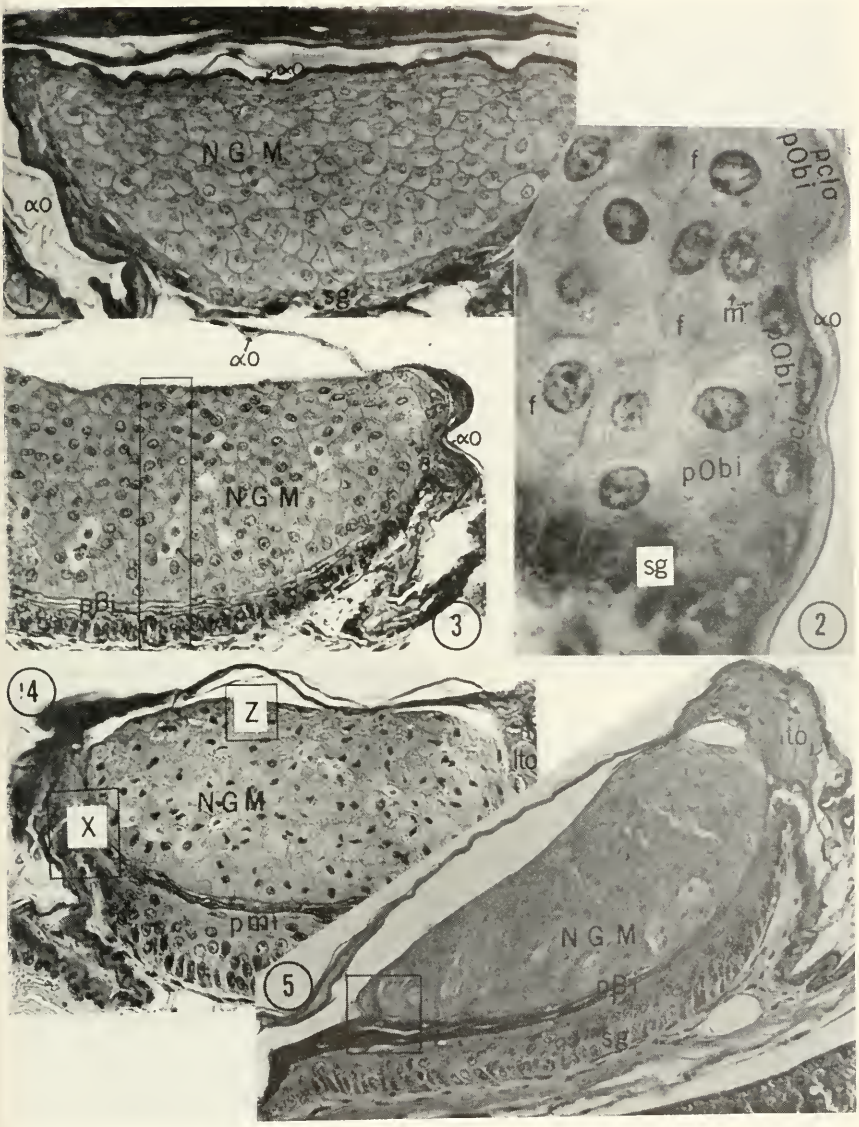
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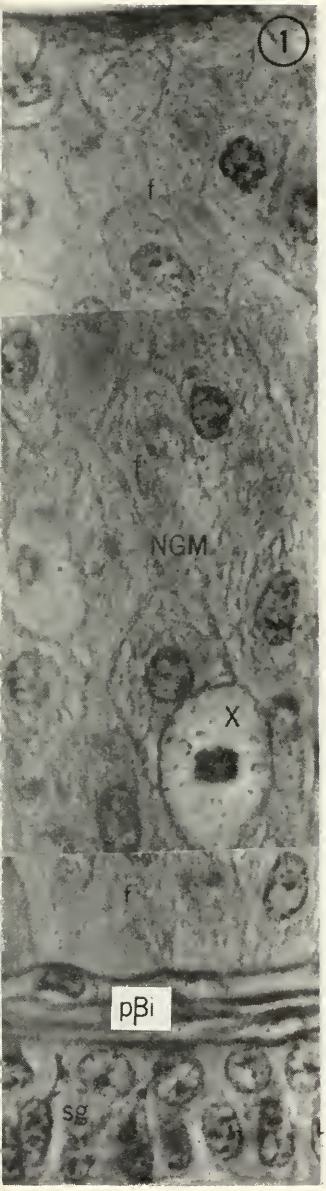
PLATE 2

PLATE 3

Figure 1. Oil montage of region indicated by rectangle in Pl. 2, fig. 3. Note the conspicuous filaments (*f*) in the more numerous cell type in the new gland material (*NGM*) and the occasional cell with granules (*X*). The outermost portion of the new gland material abuts directly onto the base of the α-layer of the outer epidermal generation (not shown).

Figure 2. Region comparable to that indicated by rectangle marked *X* in Pl. 2, fig. 4. Note the pycnotic nuclei visible in the new gland material and the sharp discontinuity of the *Oberhautchen* of the inner epidermal generation marked by an arrow.

Figure 3. Region comparable to that indicated by a rectangle in Pl. 2, fig. 5. The clear layer of the outer epidermal generation (*clo*) is recognizable by pycnotic nuclei. The sharp discontinuity of the new *Oberhautchen* is indicated by an arrow. Compare with Pl. 4, fig. 2.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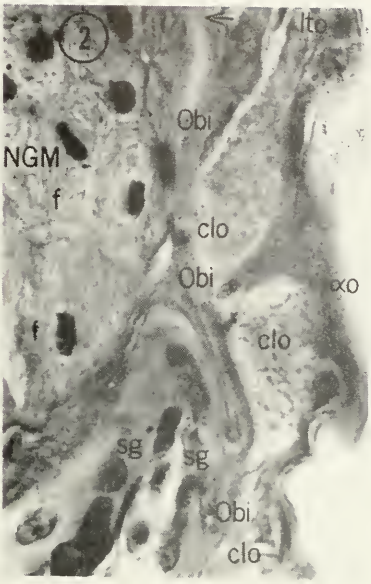
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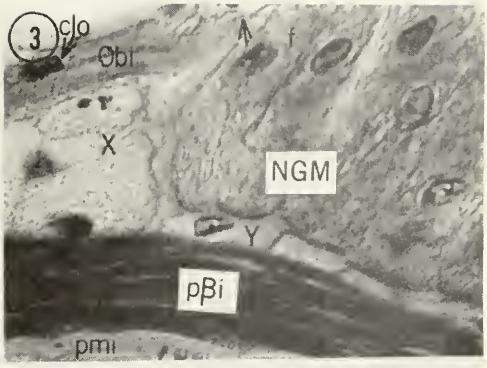
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NGM
Y
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PLATE 3

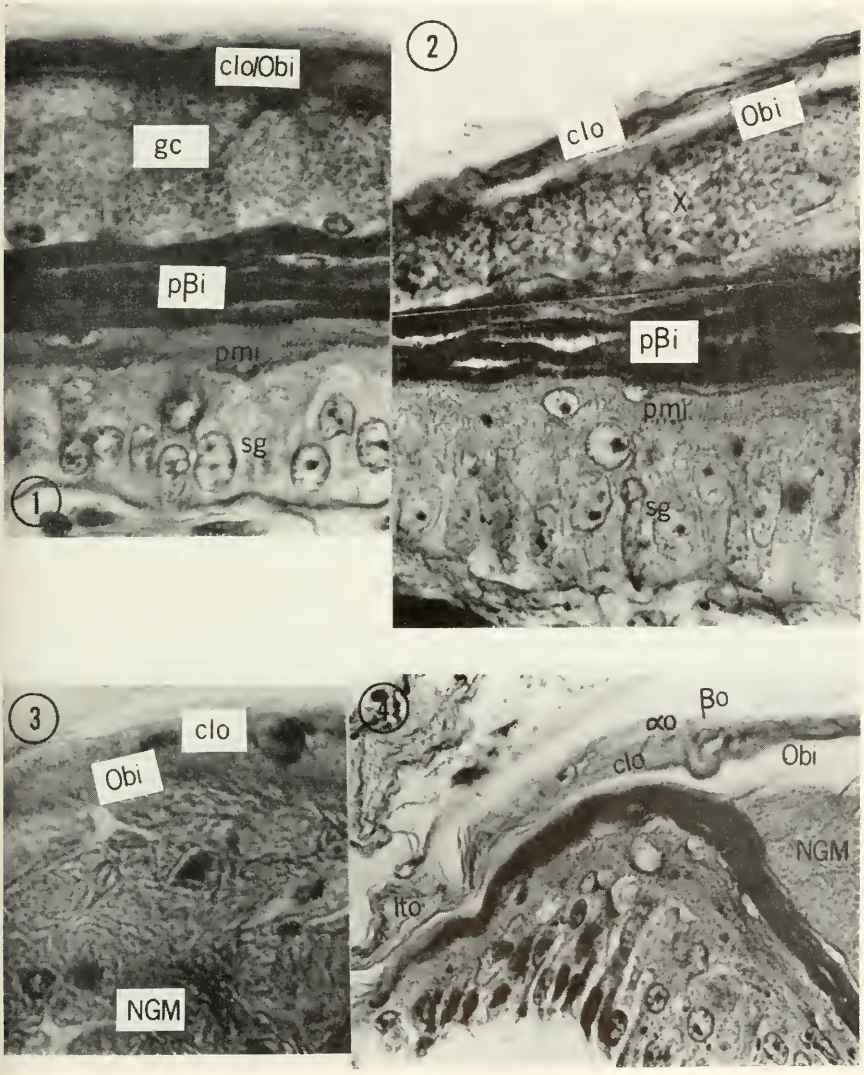
PLATE 4

Figure 1. Micrograph of epidermis from an adjacent "semi-specialized scale" showing a modification of a "Stage Four-Five" (Maderson, 1966b) with the addition of two layers of granular cells (*gc*) between the *Oberhautchen* (*Obi*) and the rest of the presumptive β-layer ($p\beta i$). Aniline blue-orange G stain.

Figure 2. Similar region of a specialized scale, as seen in sagittal section, to that shown in Pl. 3, fig. 3. This specimen shows a slightly more advanced stage of histogenesis of the new β-layer. It is readily comparable to the condition shown in figure 1 above. Note that it is possible to see where the spinules of the new *Oberhautchen* have separated from the keratinized clear layer of the outer epidermal generation. Aniline blue-orange G stain.

Figure 3. Similar region to that indicated by rectangle marked *Z* in Pl. 2, fig. 4. Hematoxylin and eosin stain.

Figure 4. Similar region to that shown in fig. 2 in an early "Condition Four." Note the chromophobic appearance of the stratum germinativum in this figure and figs. 1 and 2; this feature is characteristic of the period before, during, and after the new mesos layer is laid down. Hematoxylin and eosin stain..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αo
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clo
Obi
NGM
lto

PLATE 4

PLATE 5

Figure 1. Extreme lateral margin of specialized scale from abdominal region, seen in transverse section, showing an immediate pre-slough condition (late "Condition Four"). The β-layer of the outer epidermal generation is absent from the photograph. The new *Oberhautchen* separates from the clear layer to facilitate sloughing, to the left of the picture. In this region there is a lacunar tissue (*lto*) above the clear layer. To the right of the picture, there is no development of the lacunar tissue, clear layer, or *Oberhautchen* so that the α-layer of the outer epidermal generation (*ao*) separates directly from the new inner epidermal generation. This material will be exposed when sloughing occurs. The mesos layer (*mo*) of the inner epidermal generation has now keratinized and resembles the similar component of the outer generation. The stratum germinativum cells are regaining their chromophilic properties as the first presumptive α-cells laid down ($p \propto i$). Hematoxylin and eosin stain.

Figure 2. Plan view of a sagittal section through the scale on which the pre-anal pore opens. The rectangles marked *a*, *b*, *c*, *d* are shown in figs. 3 and 4 and Pl. 6, figs. 1 and 2, respectively. Note that the scales anterior and posterior to the scale on which the pore opens show a late "Condition Three" of the β-glands, but the scale itself is unspecialized (see figs. 3 and 4). *H* indicates direction toward head, and *T* indicates direction towards tail. Hematoxylin and eosin stain.

Figure 3. Region shown in rectangle *a* in fig. 2. This shows the epidermis in a typical Stage Four condition (Maderson, 1966b). Note the sharp discontinuity of the development of the complex epidermal generation in the mouth of the pore as shown by the arrow. The fine vertical striations indicating the old (*Obo*) and new (*Obi*) *Oberhautchen* spinules can just be seen. Several fragments of the pre-anal pore material can be seen lying in displaced positions. The lumen of the pore in this and fig. 4 (below) is indicated by *L*.

Figure 4. Region shown in rectangle *b* in fig. 2. The epidermis here shows the modified Stage Four condition (Maderson, 1966b) with a greatly reduced β-layer which characterizes the inner scale surface. Note the much-enlarged clear layer cells and the enclosed granules which may be keratohyalin (see discussion, Maderson, 1966b). Again the sharp discontinuity of the epidermal generation in the pore mouth can be seen (arrow).

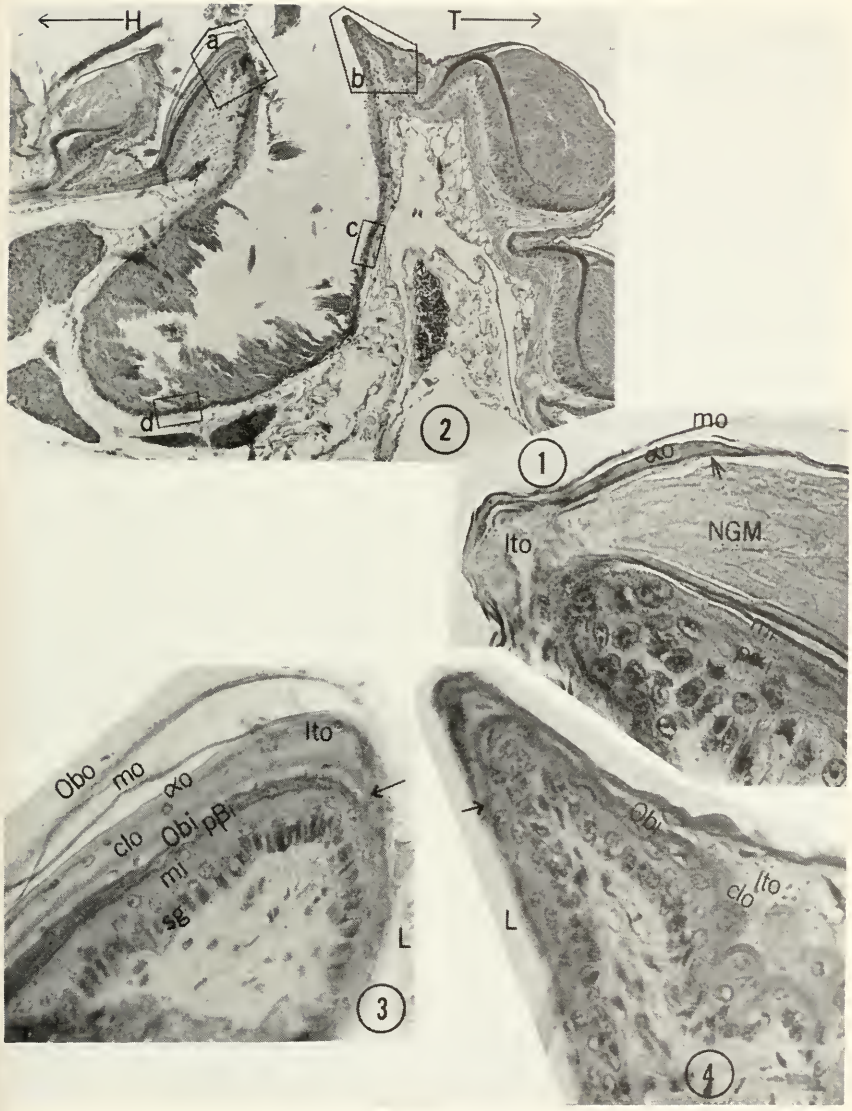
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PLATE 5

PLATE 6

Figure 1. Region indicated by rectangle *c* in Pl. 5, fig. 2. *L* indicates the lumen of the pore and *D* the dermis. Note the complete absence of any indication of "epidermal generation" structure.

Figure 2. Region indicated by rectangle *d* in Pl. 5, fig. 2. This shows the cellular elements comprising the pre-anal pore secretion which are almost fully mature and keratinized. Two pycnotic nuclei are indicated by arrows.

Figure 3. Cells in the anterior region of the forward-running pre-anal pore where the cells are immature. Note the extremely conspicuous intracellular fibrils. Aniline blue-orange G stain.

Figure 4. Cells in the extreme anterior portion of the pre-anal pore; this region is apparently the "germinal region," the site of origin of all the pore secretion. As the cells arise from the germinal layer (*sg*) they show three conspicuous features. The nucleus lies towards the germinal layer. There is a central region where fibrils are just visible (*f*) which stain intensely with orange G. There is a distal region which is occupied by a large droplet (*Dr*) which stains with aniline blue. As the cells move away from the anterior part of the gland, the droplet disintegrates, giving the picture seen in fig. 3. Aniline blue-orange G stain.

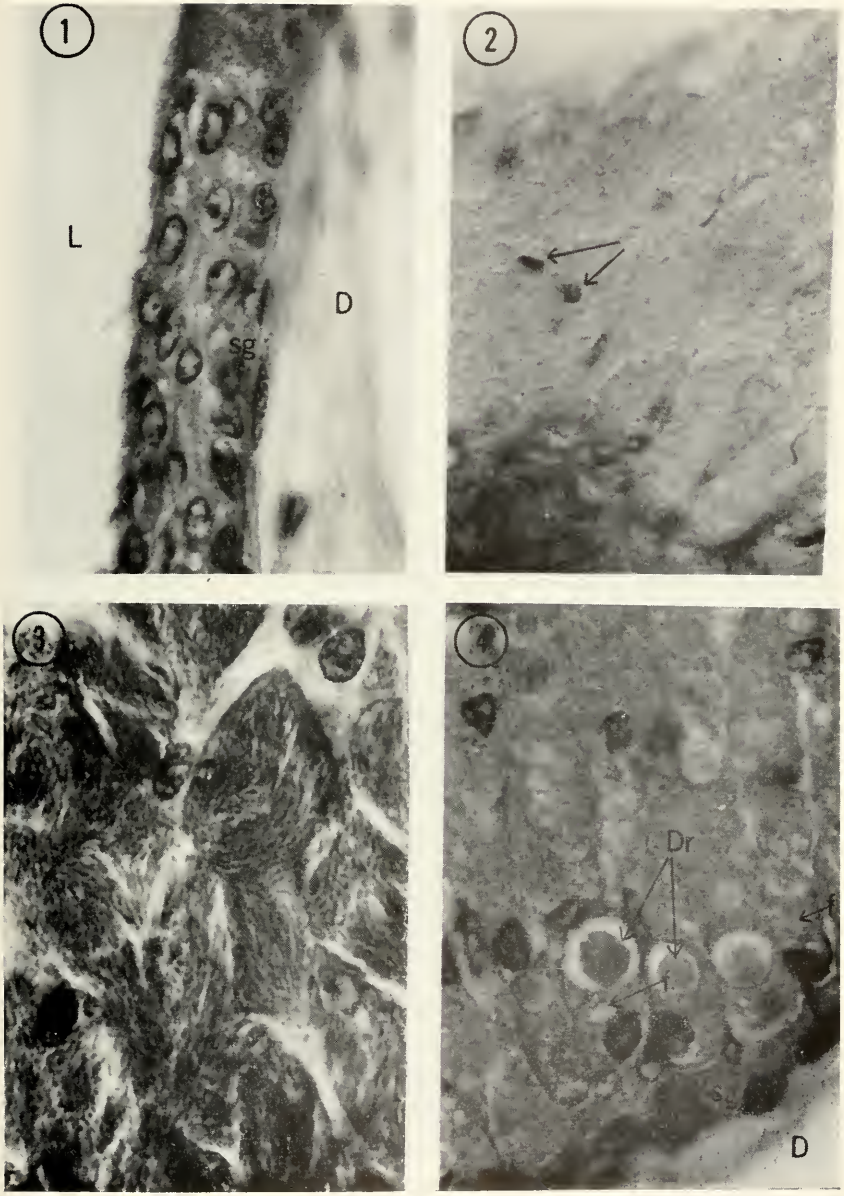


PLATE 6

BREVIORA

Museum of Comparative Zoology

CAMBRIDGE, MASS. 29 MAY, 1968 NUMBER 289

THE GENUS *MIAGRAMMOPES* (ARANEAE, ULOBORIDAE) IN PANAMA AND THE WEST INDIES

Arthur M. Chickering

The collection of members of this genus of spiders has been of interest to me for many years. As a result, I have accumulated a considerable number of specimens of both sexes from Panama and the West Indies. This seems to be a convenient time to bring together the results of this field work extending over a period of more than thirty-five years.

Up to the present time, so far as I have been able to determine, only one species of the genus has been definitely known from Panama. Mr. Banks (1929) reported the collection of *M. alboguttatus* O. P. – Cambridge on Barro Colorado Island, Canal Zone, but the specimens so identified plainly belong to *M. sinus* Chamberlin and Ivie, 1936. At present I am obliged to recognize six species of this genus from Panama. Among these are four kinds of males and four kinds of females. Although it is difficult to match males and females, I seem to be able to do this for two of the species, but four species will remain known only from a single sex until the genus can be studied more intensively.

In the West Indies, up to the present time, four species belonging to this genus have been definitely recorded. Franganillo reported *M. thwaitesii* O. P. – Cambridge from Cuba in 1936 and earlier but this identification has been shown to have been an error. For this reason this species, described originally from Ceylon, will not be further considered in this paper. At the present time I am obliged to recognize a total of nine species from the West Indies. Five are described as new to science; three of these are known only from males and the remaining two only from females.

All types, together with my entire collection of this genus, are being deposited in the Museum of Comparative Zoology, Harvard University.

Grant No GB-1801 from the National Science Foundation made it possible for me to spend seven months collecting spiders in the West Indies and Panama during the latter part of 1963 and the first five months of 1964. Grant GB-5013 from the NSF made it possible for me to spend nearly four months during 1966 collecting on nine different West Indian islands. During this time, however, I did not take a single mature specimen of *Miagrammopes*. As I have frequently stated in my published papers, I am deeply grateful for financial help from several foundations, together with help and encouragement from members of the staff of the Museum of Comparative Zoology at Harvard University over a period of many years. Special acknowledgements should be extended to Dr. Ernst Mayr, Director; Dr. P. J. Darlington, Jr., Alexander Agassiz Professor of Zoology; Dr. Herbert W. Levi, Associate Curator of Arachnology; Miss Nelda Wright, Editor of Publications; and Dr. Frank M. Carpenter, Alexander Agassiz Professor of Zoology and Editor of Psyche. My thanks are extended to Dr. G. Owen Evans and Mr. D. J. Clark, British Museum (Natural History), for the loan of very helpful specimens of *M. scoparius* Simon.

Genus Miagrammopes O. P. – Cambridge, 1870

The type species of the genus is *Miagrammopes thwaitesii* O. P. – Cambridge, 1870. The holotype is a female and is now definitely known only from Ceylon and, possibly, from India. The male remains unknown. Apparently, the P. – Cambridges had only females for the nine species described by them. The genus is now known to be widely distributed in Asia, Africa, Australia, and especially in the Neotropical region. Roewer, 1954, lists twenty-one species from the Neotropical region. Twelve of these are known only from females, two only from males, six from both sexes, and one from an immature specimen.

In addition to the general family characteristics, generic features common to the species from Panama and the West Indies, studied in the preparation of this paper, may be stated as follows: Cephalothorax in general rather low; carapace often with marked grooves and pits in the cephalic area; sternum often conspicuously subdivided and laterally extended between second and third coxae. Eyes: small; only four in number; with laterals on more or less prominent tubercles. Chelicerae of modest size, probably typically with few true teeth but with cusps and associated long hairs or bristles along margins of fang groove. Legs: 1423 in order of length

with first legs very long and quite robust; in females the first metatarsi and, to some extent, the first tibiae bear conspicuous fringes of hair; in males the first tibiae have more or less prominent batteries of robust spines; in females the fourth metatarsi and tarsi bear robust spines; the calamistrum in females extends from two-thirds to three-quarters of entire length of fourth metatarsi; in both sexes the femora appear to be well supplied with long trichobothria. In females the palpal tarsal claw is conspicuously toothed; in males the palpi are short and simple, with exception of the tarsus, which is moderately complicated. In females the abdomen is usually more or less swollen dorsally; the epigynum is often obscurely patterned.

The complete list of species of the genus *Miagrammopes* from Panama, as they are now recognized, may be given as follows: *Miagrammopes aspinatus* sp. nov.; *M. intempus* sp. nov.; *M. larundus* sp. nov.; *M. licinus* sp. nov.; *M. simus* Chamberlin and Ivie; *M. unipus* sp. nov. The complete list of species of this genus from the West Indies, as they are now recognized, may be given as follows: *M. animotus* sp. nov. from Puerto Rico; *M. ciliatus* Petrunkevitch from St. Thomas and, possibly, also from Puerto Rico; *M. cubanus* Banks from Cuba; *M. latens* Bryant from Cuba and Dominican Republic; *M. molitus* sp. nov. from Jamaica; *M. oblucus* sp. nov. from Jamaica; *M. pinopus* sp. nov. from St. John; *M. scoparius* Simon from St. Vincent; *M. tonatus* sp. nov. from Jamaica.

Key to the males of known species of MIAGRAMMOPES *from Panama and the West Indies*

1a. Species in which the carapace is nearly or quite as wide as long (*aspinatus, simus, unipus*) 2
1b. Species in which the carapace is clearly longer than wide (*animotus, latens, licinus, molitus, scoparius, tonatus*) 4
2a. Palpal tarsus with three prominent, terminal apophyses (Fig. 10) ..... *M. aspinatus*
2b. Palpal tarsus lacking the three prominent terminal apophyses (*simus, unipus*) 3
3a. First tibia armed with a battery of about 21-22 robust, erect spines extending nearly the entire length of the segment (Fig. 43). *M. simus*
3b. First tibia with fewer and weaker spines extending through about the distal two-thirds of the segment (Fig. 50) ..... *M. unipus*
4a. Carapace about twice as wide at level of lateral eyes as at posterior end where is it squarely truncate (Fig. 24) ..... *M. molitus*
4b. Carapace less than twice as wide at level of lateral eyes as at posterior end (*animotus, latens, licinus, scoparius, tonatus*) 5
5a. Palpal tibia concave dorsally; first tibia with very few spines as seen in retrolateral view (Figs. 20-23) ..... *M. licinus*

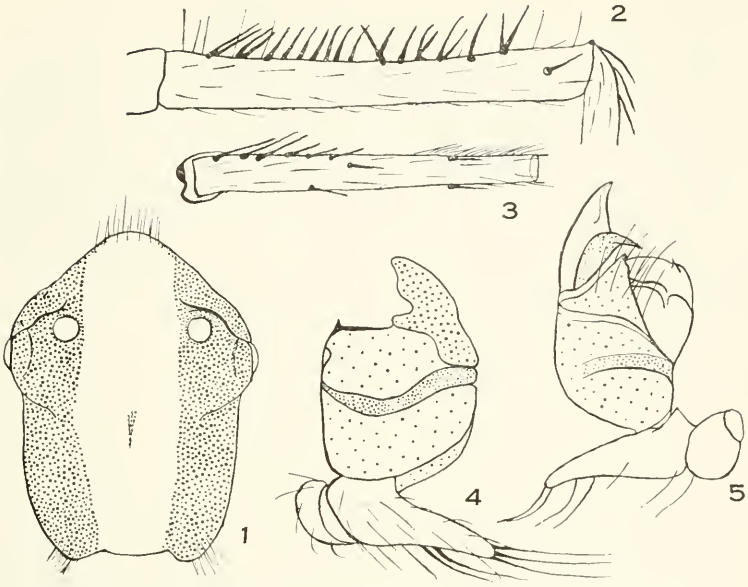
5b. Species lacking such a combination of features as given above (*animotus, latens, scoparius, tonatus*) 6
6a. Carapace nearly rectangular in outline in posterior two-thirds; first tibia with few long spines showing in retrolateral view (Figs. 45, 46) ..... *M. tonatus*
6b. Species without combination of features given above (*animotus, latens, scoparius*) 7
7a. Carapace with a broad, white, median stripe throughout; palpal tarsus with a pair of robust, distal apophyses; first tibia with numerous dorsal spines (Figs. 1, 2, 5) ..... *M. animotus*
7b. Species lacking such a combination of features as given above (*latens, scoparius*) 8
8a. Palpal tarsus terminating in a single robust apophysis together with a series of small, sharply pointed spines (Bryant, 1936, fig. 4) ..... *M. latens*
8b. Palpal tarsus with a distal apophysis divided into a robust hook and a slender, sickle-shaped extension (Fig. 36) ..... *M. scoparius*

Miagrammopes animotus sp. nov.

Figures 1-5

Holotype. The male is from Mayaguez, Puerto Rico, W. I., in a wooded area near Nuclear Center, January 27, 1964. The name of the species is an arbitrary combination of letters.

Description. Total length from anterior border of carapace to posterior end of spinnerets about 2.8 mm (body curled). Carapace 0.97 mm long; 0.71 mm wide at level of lateral ocular tubercles where it is widest; with little hair; only a slight depression to represent the median thoracic fovea; grooves and depressions in ocular region, so conspicuous in some species, only slightly developed here; lateral ocular tubercles also weakly developed (Fig. 1). Eyes: only four, in a gently recurved row as seen from above; ratio of eyes ME : LE = about 6 : 7; ME separated from one another by about 4.6 times their diameter, from LE by a little less than three times their diameter; with very little black pigment in ocular region. Chelicerae, maxillae, and lip difficult to observe closely but apparently typical of males of the genus. Sternum: very much swollen in middle and greatly expanded between second and third coxae; in general, typical of males of the genus. Legs: tibial index of first leg 12, of fourth leg 10; first leg with a conspicuous battery of stout spines on tibia and metatarsus (Figs. 2-3); first leg somewhat more than twice as long as second leg and a little more than three times as long as third leg. Calamistrum lacking. Palp: essential features



Figures 1-5. *Miagrammopes animotus* sp. nov. Fig. 1. Carapace; from above. Fig. 2. Right first tibia; retrolateral view. Fig. 3. Right first metatarsus; dorsal view (several spines restored from scars). Figs. 4-5. Male palp; retrolateral and prolateral views, respectively.

shown in Figures 4-5. Abdomen without special features; apparently quite typical of males of the genus. Color in alcohol: carapace with a broad, median, white stripe covering the median third from clypeus to posterior border; lateral thirds of the carapace brownish gray with black, irregular, short lines; sternum yellowish with irregular grayish spots; legs generally yellowish but first legs are brown dorsally; abdomen with nearly the whole dorsum light yellowish with white flecks; a pair of minute black dots occurs on the dorsum a little in front of the middle and another pair of black dots occurs a little behind the middle of the dorsum; a black, lateral stripe on each side extends the whole length of the abdomen; the central part of the venter is very light brownish and the remainder is nearly the same but with many whitish flecks.

Records. Two immature specimens taken on the same day as the holotype and in the same locality are tentatively placed in this species, but their identification must remain uncertain.

Miagrammopes aspinatus sp. nov.

Figures 6-10

Holotype. The male is from Barro Colorado Island, Panama Canal Zone, June, 1950. The name of the species is an arbitrary combination of letters.

Description. Total length from anterior border of carapace to posterior end of extended spinnerets about 3.82 mm. Carapace about 1.29 mm long; 1.21 mm wide at level of lateral ocular tubercles where it is widest; about 0.57 mm tall; quite hairy; with moderately well developed median thoracic fovea, pits and grooves in ocular regions and lateral ocular tubercles (Fig. 6). Eyes: only four, as usual in the genus; with the row slightly recurved as seen from above; ratio of eyes ME : LE = 6 : 7.5; ME separated from one another by about nine times their diameter, from LE by about five times their diameter. Chelicerae, maxillae and lip apparently typical of males of the genus but details not clearly observed because of fragility of holotype and closely coiled appendages. Sternum: quite typical in general; quite convex in middle but less so than in some species; much narrowed at posterior end and, apparently, continued by an extra, very narrow sclerite between fourth coxae, which are separated by slightly more than one-fifth of their width. Legs: tibial index of first leg 11, of fourth leg 12; first leg nearly twice as long as second leg; nearly three times as long as third leg; first tibia with a conspicuous battery of robust spines much as in *M. simus* Chamberlin and Ivie; fourth tibia also with numerous long, stout spines (Figs. 7-8). Palp: essential features shown in Figures 9-10; tibia with quite distinctive form. Abdomen: typical of males of the genus. Color in alcohol: yellowish throughout with some variation; only a moderate amount of black pigment in ocular region; abdomen with three pairs of minute dots on dorsum equally spaced from the base; legs with few gray areas.

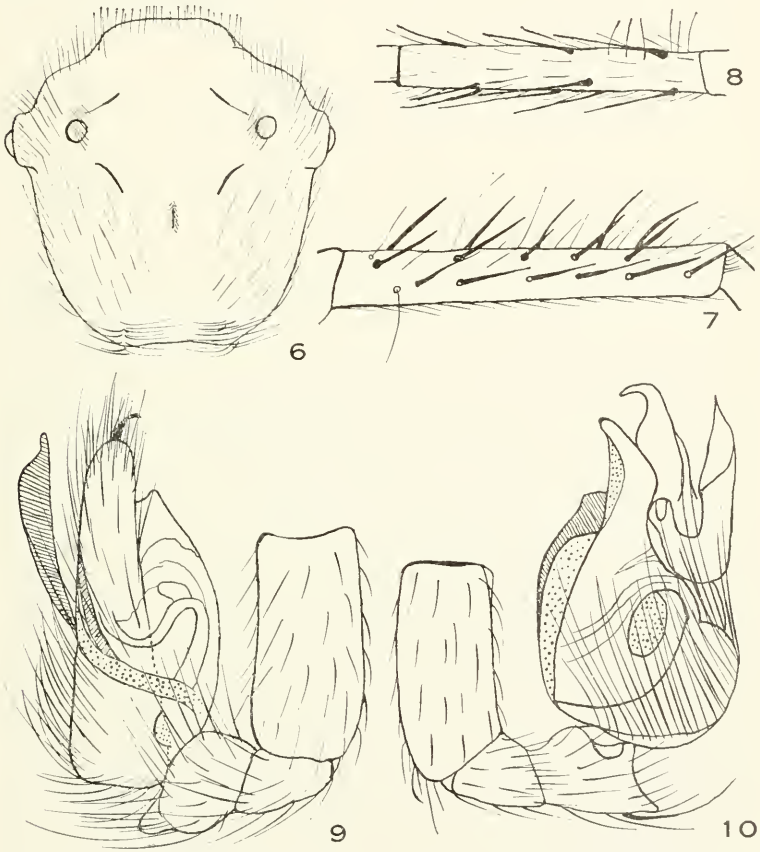
Records. The female is unknown. Another specimen of the genus was taken at the same time and in the same locality as the holotype, but it is immature and its identification is very uncertain.

Miagrammopes ciliatus Petrunkevitch

Miagrammopes ciliatus Petrunkevitch, 1926: 47, fig. 7. The present location of the holotype is quite uncertain. Petrunkevitch, 1930: 232; Roewer, 1954: 1349; Bonnet, 1957: 2830.

The holotype of this species was a female from St. Thomas, U. S. Virgin Islands, collected in July, 1915. No description of the epigynum was given. Dr. Petrunkevitch later had several specimens of

what he assumed to be the same species from Puerto Rico. Among these were three females regarded as mature and several immature specimens of both sexes. I think it unlikely that the Puerto Rican specimens belong to *M. ciliatus* Petrunkevitch but I cannot be positive at this time. In my collection from Puerto Rico, made in January and February, 1964, I have a single mature male and several immature specimens but not a single mature female. The mature male is being described as a new species elsewhere in this paper.



Figures 6-10. *Miagrammopes aspinatus* sp. nov. Fig. 6. Carapace; from above. Fig. 7. Right first tibia; dorso-retrolateral view. Fig. 8. Right fourth tibia; prolateral view. Figs. 9-10. Male palp; prolateral and retrolateral views, respectively.

Miagrammopes cubanus Banks

Miagrammopes cubanus Banks, 1909: 159. The holotype is in the Museum of Comparative Zoology. Bryant, 1940: 329; Roewer, 1954: 1349; Bonnet, 1957: 2830.

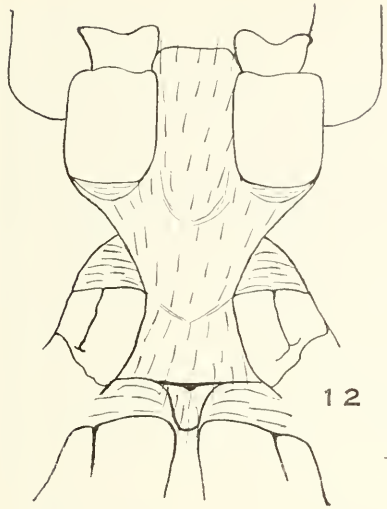
The holotype was very briefly described and no figures were published. The holotype is immature and its status cannot be determined until careful collecting is pursued in the type locality. Miss Bryant (1940) stated that *M. latens* Bryant might prove to be a synonym for *M. cubanus* Banks. A few specimens assigned to *M. cubanus* Banks since the holotype was described are plainly *M. latens* Bryant.

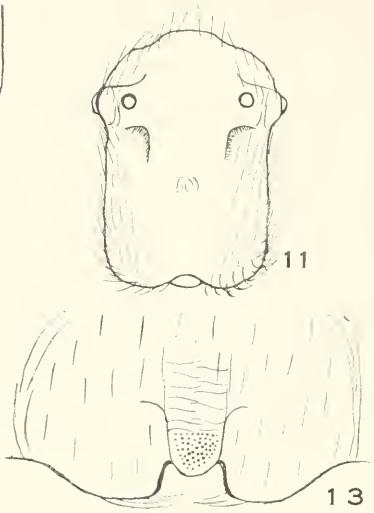
Miagrammopes intempus sp. nov.

Figures 11-13

Holotype. The female is from Porto Bello, Panama, August 11, 1936. The name of the species is an arbitrary combination of letters.

Description. Total length from anterior border of porrect chelicerae to posterior end of spinnerets 6.24 mm; length from anterior border of carapace to posterior end of anal tubercle 5.85 mm. Carapace 1.54 mm long; 1.08 mm wide at level of lateral ocular tubercles where it is widest; grooved behind ME in somewhat distinctive manner; with a poorly defined median thoracic fovea (Fig. 11); about 0.55 mm tall; lateral ocular tubercles less prominent than in some other species; with many hairs. Eyes: four as usual, in a slightly recurved row as seen from above; ratio of eyes ME : LE = 6.5 : 8; ME separated from one another by about eight times their diameter, from LE by nearly 3.5 times their diameter. Chelicerae, maxillae and lip apparently quite typical of females of the genus. Sternum: conspicuously distinctive; anterior portion sharply narrowed from median portion which is greatly widened and extended between second and third coxae thus forcing first and second legs forward and third and fourth legs backward; between third and fourth coxae there is a transverse shelf and behind this a greatly depressed and narrowed portion (Fig. 12); in front of third coxae are loose, membranous structures and just behind second coxae are smaller, similar structures; fourth coxae separated by slightly less than one-fourth their width. Legs: tibial index of first leg 13, of fourth leg 10; first leg with copious hair fringes on tibia and metatarsus; first leg nearly twice as long as second leg and about 2.5 times as long as third leg; fourth tibia a little longer than first tibia; second and third coxae very widely





Figures 11-13. *Miagrammopes intempus* sp. nov. Fig. 11. Carapace; dorsal view. Fig. 12. Sternum, seen from below. Fig. 13. Epigynum, seen from below.

separated as already noted; only occasional slender spines on palps and legs with exception of fourth tarsi and metatarsi where special, short, robust spines occur similar to those figured for *M. simus* Chamberlin and Ivie. Black palpal claw quite conspicuous. Calamistrum about three-fourths as long as fourth metatarsus. Abdomen with a conspicuous dorsal hump a little in front of the middle; otherwise apparently quite typical of females of the genus. Epigynum: essentials shown in Figure 13. Color in alcohol: carapace light brownish in general but with many darker streaks; lighter through the center and darker along lateral sides; sternum light yellowish brown; legs brownish in general with first pair darkest on dorsal surfaces and light brownish below; abdomen with a dark median stripe widest in anterior third then narrowed at top of dorsal hump and widened again at posterior end; each side of the central dark stripe there is a lighter, finely reticulated area; these reticulated areas continue laterally and nearly throughout the venter; a grayish area on each lateral side of the abdomen extends backward from the base to nearly opposite the dorsal hump.

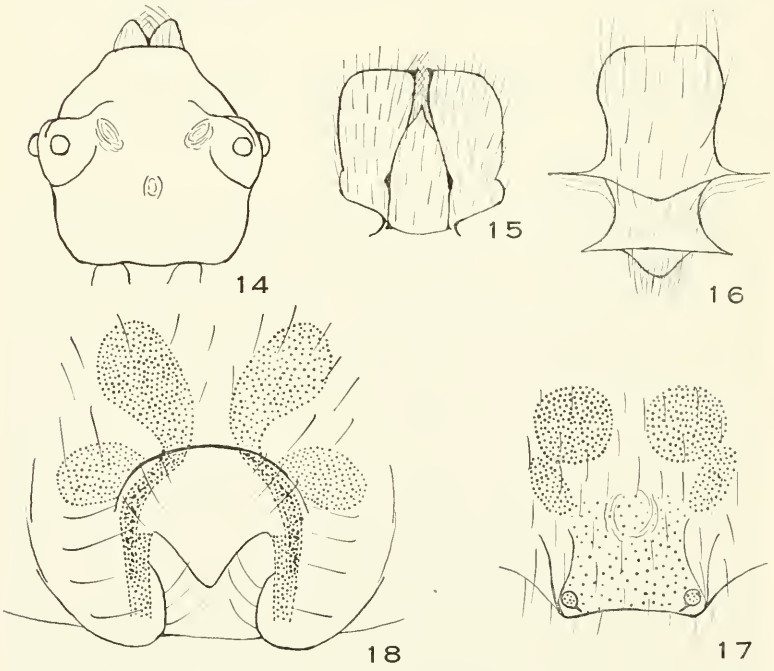
Records. The male is not known and there are no female paratypes.

MIAGRAMMOPES LARUNDUS sp. nov.

Figures 14-17

Holotype. The female is from Barro Colorado Island, Panama Canal Zone, August, 1950. The name of the species is an arbitrary combination of letters.

Description. Total length from anterior border of extended chelicerae to posterior end of spinnerets 4.92 mm. Carapace 1.23 mm long; 1.32 mm wide at level of lateral ocular tubercles where it is widest; 0.45 mm tall at level of eyes where it is tallest; with grooves and depressions well developed (Fig. 14); depressions medial to ME deep and conspicuous; division and course of grooves around ocular regions somewhat complicated; median thoracic fovea hardly discernible; with a fairly well developed coat of short hair directed forward. Eyes: four as usual, in a slightly procurved row as seen from above; ratio of eyes ME : LE = 10 : 11; ME separated from



Figures. 14-17. *Miagrammopes larundus* sp. nov. Fig. 14. Carapace, dorsal view. Fig. 15. Maxillae and lip. Fig. 16. Sternum, seen from below. Fig. 17. Epigynum, seen from below. Fig. 18. *Miagrammopes latens* Bryant. Epigynum, seen from below.

one another by nearly nine times their diameter; separated from LE by about 1.3 times their diameter; with black pigment nearly covering the ocular tubercles. Chelicerae: apparently typical of females of the genus. Maxillae, lip and sternum with features as shown in Figures 15-16. Legs: tibial index of first leg 10, of fourth leg 9; calamistrum as usual in females of the genus; fourth metatarsus and tarsus with the short, stout spines similar to those figured for *M. simus* Chamberlin and Ivie; first leg nearly twice as long as second leg and nearly three times as long as third leg. Abdomen without a dorsal, medial swelling such as frequently occurs in females of the genus; otherwise typical of females of the genus and without noteworthy features. Epigynum: obscurely distinctive; observable features shown in Figure 17. Color in alcohol: carapace with most of dorsum light yellowish brown but with numerous gray streaks and spots; lateral areas gray with considerable black pigment in ocular regions; sternum light grayish with a yellowish median stripe; mouth parts generally yellowish with a few grayish spots; legs generally brownish. Abdomen with a conglomerate color pattern; anterior two-thirds of dorsum yellowish, irregularly reticulated and with two pairs of irregularly shaped darker, oblique spots; posterior end of abdomen irregularly brown; lateral sides with several long, narrow, alternating, irregular light and dark lines; venter brownish with a series of stripes leading from genital groove to near the posterior end; there is a narrow, indefinite, brownish, central stripe, a pair of pale, narrow stripes, a pair of broader brownish stripes, and a pair of light lines most lateral of all.

Records. A female collected on May 5, 1964, in the type locality appears to be a paratype; an immature male and an immature female also collected in the type locality at about the same time probably belong to this species.

MIAGRAMMOPES LATENS Bryant

Figure 18

Miagrammopes latens Bryant, 1936: 326, pl. 23, fig. 4. The holotype male is in the Museum of Comparative Zoology; it was taken in Cuba, Sierra del Cobre, Loma del Gato. Bryant, 1940: 330; 1948: 393; Roewer, 1954: 1350; Bonnet, 1957: 2831.

The holotype male is from the mountains of Cuba; the palp is still in good condition and well represented by Miss Bryant's plate 23, figure 4. I have not been able to find the specimen regarded by Miss Bryant as the allotype but I have studied a female from the same locality and, apparently, taken with the allotype. My Figure

18 is taken from this specimen. I see the epigynum somewhat differently than represented by Miss Bryant's figure 98 (1940); I have noted, however, considerable variation in the appearance of this organ among available specimens assigned to this species. The matter will probably not be clarified until numerous specimens are available for study following extensive collecting in the regions where the species occurs.

Miagrammopes licinus sp. nov.

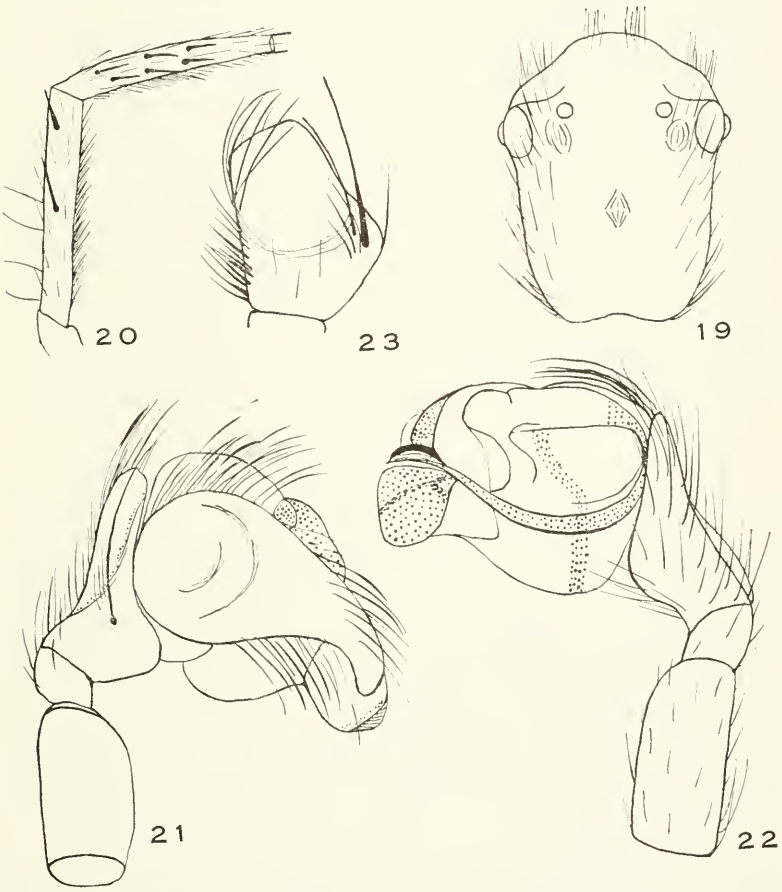
Figures 19-23

Holotype. The male is from El Volcan, Panama, August 14, 1950. The name of the species is an arbitrary combination of letters.

Description. Total length from anterior border of slightly porrect chelicerae to posterior end of spinnerets 3.32 mm. Carapace 1.19 mm long; 0.84 mm wide at level of ocular tubercles; 0.48 mm tall; ocular tubercles quite well delineated by grooves; with a fairly well defined median thoracic fovea; with a pair of depressions shortly behind ME; with a fairly well developed coat of hair which appears whitish in the light used for description (Fig. 19). Eyes: four as usual, in a gently recurved row as seen from above; ME separated from one another by seven times their diameter, from LE by slightly more than four times their diameter; ratio of eyes ME : LE = 5 : 7. Chelicerae, maxillae and lip: all apparently typical of males of the genus. Sternum: extremely convex in the middle; fourth coxae contiguous. Legs: tibial index of first leg 12, of fourth leg 13; first tibia with few spines (Fig. 20) and with different numbers on right and left; first metatarsus with spines as shown in Figure 20; first leg slightly more than twice as long as second leg and nearly three times as long as third leg; the calamistrum is lacking but the fourth metatarsus and tarsus bear several robust, ventral spines similar to those which occur on females; tarsal claws as usual. Palp: general features shown in Figures 21-23; the tibia is very distinctive with its dorsal expansion and concavity; copiously supplied with slender spines; tarsus complicated with its parts difficult to distinguish. Abdomen: without special features; apparently typical of males of the genus. Color in alcohol; carapace with a yellowish, median, longitudinal stripe about one-third as wide as this part of the body; this yellowish stripe contains a narrow, grayish stripe which widens near the middle into an irregular diamond-shaped figure; a broad dark gray stripe covers the remainder of the carapace on each side; sternum yellowish; abdomen with a fairly broad,

grayish, central, dorsal stripe indented along two-thirds of its length and then irregularly broken into a series of five or six somewhat separate spots; on each side of this central stripe there is a yellowish stripe; lateral sides of abdomen irregularly dark grayish; the venter has a grayish central stripe and on each side a narrow, light yellowish stripe and a narrow, darker stripe; all five of these ventral stripes are quite inconspicuous; legs in general yellowish; first pair with considerable dark gray coloration on dorsal and prolateral surfaces.

Records. The female is unknown and there are no paratypes.

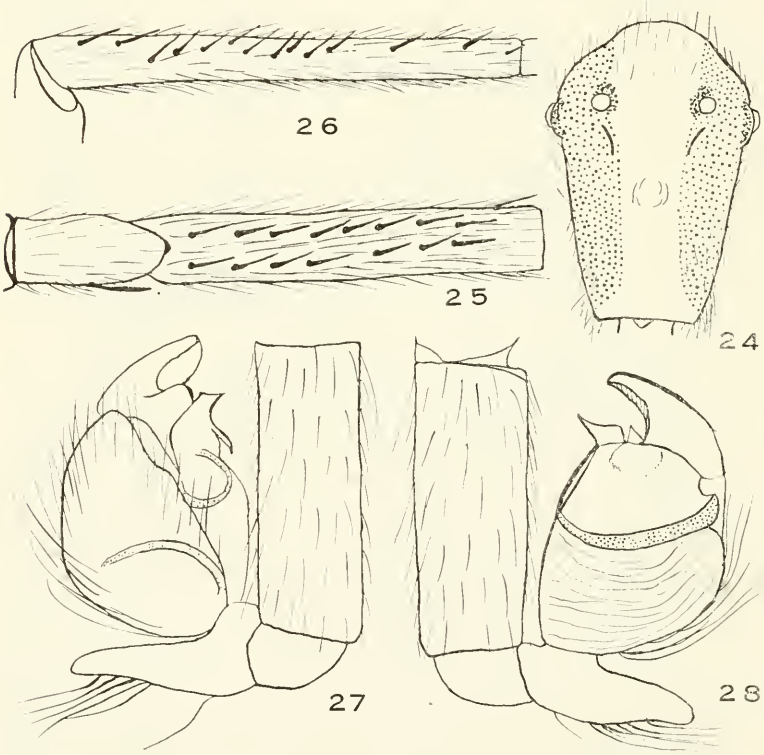


Figures 19-23. *Miagrammopes licinus* sp. nov. Fig. 19. Carapace, dorsal view. Fig. 20. Right first tibia and metatarsus; retrolateral view. Figs. 21-22. Left palp; prolateral and retrolateral views, respectively. Fig. 23. Left palpal tibia; dorsal view.

MIAGRAMMOPES MOLITUS sp. nov.
Figures 24-28

Holotype. The male is from Jamaica, W. I., Portland Parish, Hardwar Gap, October 2, 1957. The name of the species is an arbitrary combination of letters.

Description. Total length about 3.15 mm (body curled closely). Carapace 1.17 mm long; 0.81 mm wide at level of lateral ocular tubercles; about 0.44 mm tall at level of median eyes where it is tallest; with median thoracic fovea barely indicated; with grooves in ocular region very obscure (Fig. 24). Eyes: four as usual with row gently recurved; ratio of eyes ME : LE = 6 : 7; ME separated from



Figures 24-28. *Miagrammopes molitus* sp. nov. Fig. 24. Carapace, dorsal view. Fig. 25. Left first tibia and patella; dorsal view. Fig. 26. Left first metatarsus; prolateral view. Figs. 27-28. Left male palp; prolateral and retrolateral views, respectively.

one another by slightly more than five times their diameter, from LE by about 3.3 times their diameter; with only a moderate amount of black pigment around eyes. Chelicerae, maxillae, lip and sternum impossible to observe clearly because of sharply curled position of holotype and its fragility. Legs: tibial index of first leg 11, of fourth leg 10; first leg with a series of spines on tibia and metatarsus as shown in Figures 25-26; these spines are less robust and have a different placement than in other species treated in this study; other legs with few or no spines but with a copious hair covering; no true fringes observed; first legs considerably more than twice as long as second legs, three times as long as third legs and 1.7 times as long as fourth legs. Palp: complicated; parts difficult to observe because of transparency; form essentially as shown in Figures 27-28. Abdomen: apparently quite typical of males of the genus. Color in alcohol; carapace with a broad, yellowish, median stripe extending the whole length of this part of the body and occupying the middle third; lateral thirds of the carapace grayish brown; sternum yellowish; legs in general yellowish but first legs somewhat grayish brown along dorsal surfaces; abdomen with a median, dorsal, yellowish, longitudinal stripe and a narrower grayish stripe on each side; remainder of the abdomen yellowish with variations.

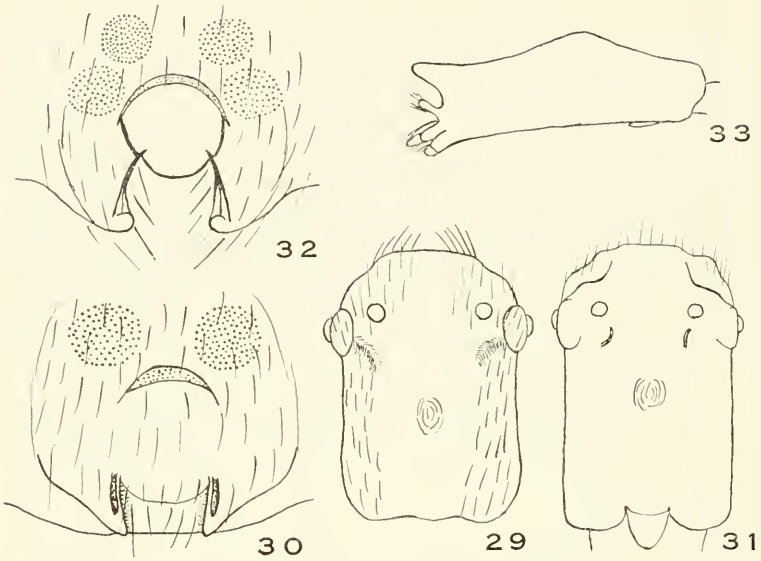
Records. The female is unknown; there are no male paratypes; an immature specimen was taken in the same locality and on the same day as the holotype but its identification is uncertain.

MIAGRAMMOPES OBLUCUS sp. nov.

Figures 29-30

Holotype. The female is from Jamaica, Portland Parish, Hardwar Gap, November 22, 1957. The name of the species is an arbitrary combination of letters.

Description. Total length from anterior border of somewhat extended chelicerae to posterior end of spinnerets about 5.57 mm (body considerably curled). Carapace 1.58 mm long; 1.12 mm wide at level of lateral ocular tubercles where it is widest; about 0.55 mm tall; median thoracic fovea barely discernible; with a moderately developed coat of hair (Fig. 29). Eyes: four as usual, in a gently recurved row, seen from above; ratio of eyes ME : LE = 8 : 10; ME separated from one another by nearly 6.25 times their diameter, from LE by about 3.5 times their diameter. Chelicerae, maxillae and lip apparently quite typical of females of the genus. Sternum: essentially as described for *M. sinus* Chamberlin and Ivie except that there is an angular distortion at the swollen and



Figures 29-30. *Miagrammopes oblucus* sp. nov. Fig. 29. Carapace; from above. Fig. 30. Epigynum; seen from below. Figs. 31-33. *Miagrammopes pinopus* sp. nov. Fig. 31. Carapace; dorsal view. Fig. 32. Epigynum; seen from below. Fig. 33. Abdomen; lateral view, right side.

expanded median part; posterior end not clearly visible but appears to terminate in a narrow, rounded point. Legs: tibial index of first leg 12; of fourth leg 8; first leg slightly more than twice as long as second leg, nearly three times as long as third leg and about 1.4 times as long as fourth leg; calamistrum extends over about five-sixths of the length of the fourth metatarsus; first metatarsus with a definite dorsal fringe; fourth metatarsus and tarsus each with a row of short spines on ventrolateral surface essentially as in *M. sinus* Chamberlin and Ivie (Fig. 40). Abdomen: robust, with a slight swelling a little in front of the middle; otherwise quite typical of females of the genus as observed in this study. Epigynum: somewhat obscure; essential observed features shown in Figure 30. Color in alcohol: carapace generally grayish brown; with a lighter, median, irregular stripe extending the entire length of this part of the body; the lateral thirds darker and with a narrow, marginal white stripe. Sternum light yellowish brown. Mouth parts yellowish with variations; the lip is largely grayish. Legs: yellowish in general; first and

second legs with dorsal and dorsolateral surfaces dark grayish brown; fourth metatarsus dark dorsally and prolaterally. Abdomen: with a central, dorsal, very irregular brownish gray stripe flanked on each side by a lighter, irregular stripe; a pair of black dots is present on the dorsum somewhat in front of the middle, and another pair of black dots occurs just behind the middle; lateral sides irregularly brownish; the venter is a kind of light, reddish brown with a narrow, central stripe flanked on each side by a narrow lighter stripe; two pairs of black dots appear in the posterior half of the venter.

Records. The male is unknown. One female was taken on the same day and in the same general locality as the holotype and is tentatively regarded as a paratype, but there are differences which may be due to immaturity.

MIAGRAMMOPES PINOPUS sp. nov.

Figures 31-33

Holotype. The female is from St. John, U. S. Virgin Islands, Centerline Road, 4 miles east of Cruz Bay, March 4, 1964. The name of the species is an arbitrary combination of letters.

Description. Total length from anterior border of extended chelicerae to posterior end of extended abdomen 6.9 mm. Carapace: 1.76 mm long; 1.07 mm wide at level of lateral ocular tubercles; about 0.55 mm tall; with grooves in ocular region only moderately developed; with median thoracic fovea shallow and inconspicuous (Fig. 31). Eyes: four as usual, in a gently recurved row; ratio of eyes ME : LE = 6.5 : 7; ME separated from one another by about seven times their diameter, from LE by slightly more than half that distance. Chelicerae and maxillae apparently typical of females of the genus. Lip: long, slender, convex; widest just before the middle; distal end a fine point. Sternum: long, slender, except for excessive width between second and third coxae; narrowest between first and second coxae; posterior end very hairy, somewhat tuberculate, rounded and ending just opposite bases of fourth coxae, which are separated by a little more than one-third of their width. Legs: tibial index of first leg 11, of fourth leg 7; first leg slightly more than twice as long as second leg, somewhat less than three times as long as third leg, and about 1.4 times as long as fourth leg; all tarsi with claws as usual; calamistrum as usual in females of the genus; fourth metatarsus and tarsus with spines essentially as shown in Figure 40 for *M. sinus* Chamberlin and Ivie; other spines seem to be lacking on legs. Palp: with well developed claw and with about five long, slender teeth. Abdomen: moderately raised dorsally; with posterior

end continued into a definite caudal extension above anal tubercle (Fig. 33) and spinnerets; otherwise typical of females of the genus. Epigynum: essential features shown in Figure 32; quite distinctive; resembles that of *M. latens* Bryant. Color in alcohol: carapace grayish brown with many narrow, darker, irregular lines and spots and with lateral sides somewhat lighter; sternum yellowish brown; legs generally yellowish with first pair gray on dorsal surfaces; mouth parts yellowish. Abdomen: light yellowish in general; very reticulate; with a grayish brown, broken stripe along the median dorsal region and with lateral regions bearing irregular and poorly defined, darker, oblique bands; venter highly reticulate and with a pair of very narrow, dark stripes extending from epigynum to the vicinity of the cribellum.

Records. The male is unknown; there are no female paratypes.

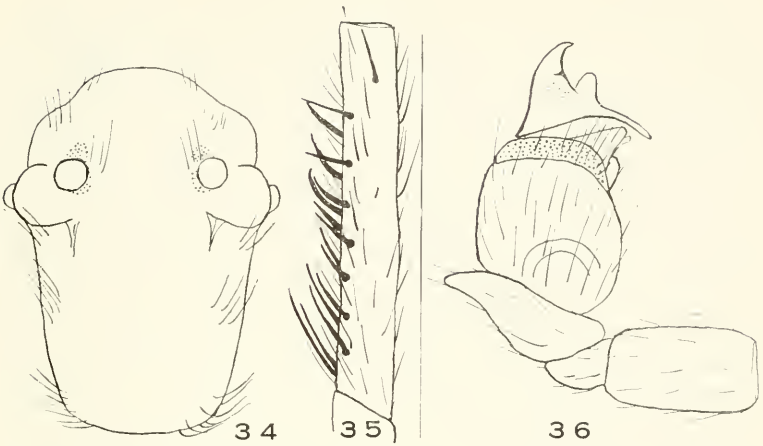
Miagrammopes scoparius Simon

Figures 34-36

Miagrammopes scoparius Simon, 1891: 555. The types, male and female, are in the British Museum (Natural History) and were taken on St. Vincent, B.W.I. Simon, 1892: 220; Petrunkevitch, 1911: 97; 1930: 232; Lutz, 1915: 79; Roewer, 1954: 1350; Bonnet, 1957: 2831.

Lutz (1915) reported this species from Puerto Rico, but this is now regarded as an error in identification and, apparently, the species is known only from the type locality. No figures were published with the original description, but in 1902 Simon published a figure of the male palp (fig. 164). Through the courtesy of the Department of Zoology, British Museum (Natural History), I have been able to examine eight specimens from St. Vincent. Three of these are males and one of them has been selected for brief description as given below. The five females all appear to be in various stages of immaturity and, for this reason, no detailed description has been prepared.

Male. Total length about 3.2 mm (body somewhat curled). Carapace 1.1 mm long; 0.79 mm wide at level of LE; general appearance as shown in Figure 34. Simon gave length of male as 4.5 mm. Eyes: four as usual, in a recurved row as seen from above; ME separated from one another by 4.6 times their diameter, separated from LE by about 2.25 times their diameter; ratio of eyes ME : LE = 7 : 8. Chelicerae, maxillae, lip and sternum apparently all typical of males of the genus. Legs: 1423 in order of length; first leg more than twice as long as second leg, more than three times as long as third leg but a little less than twice as long as



Figures 34-36. *Miagrammopes scoparius* Simon. Fig. 34. Carapace of male from above. Fig. 35. First right tibia; retrolateral view. Fig. 36. Left palpus of male; prolateral view.

fourth leg. Tibial index of first leg 11, of fourth leg 9. First tibia with a conspicuous battery of robust spines (Fig. 35). Calamistrum lacking; present in immature male. Palp: essential features shown in Figure 36. Abdomen: typical of the genus; without unusual features. Color in alcohol: carapace light yellowish brown in general, somewhat lighter in middle of anterior half; whole area irregularly reticulated with fine dark lines; legs yellowish in general with variations; first leg grayish dorsally; abdomen yellowish through the center and grayish along lateral sides with venter yellowish.

Females. As already indicated, the five females accompanying the males seem to be immature with no developed epigyna. Their general appearance agrees quite well with that of the males. The largest female has a total length of about 4.22 mm (Simon gave length of female as 6 mm).

MIAGRAMMOPES SIMUS Chamberlin and Ivie

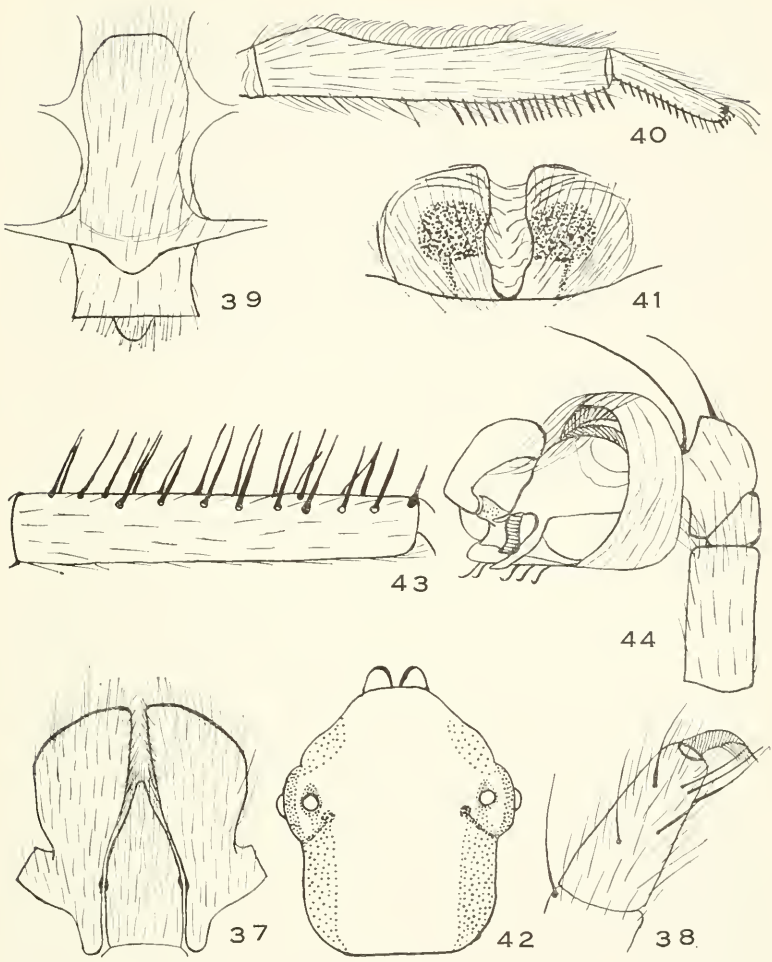
Figures 37-44

Miagrammopes simus Chamberlin and Ivie, 1936: 12, pl. 2, figs. 11-12. The female holotype from Barro Colorado Island, Panama Canal Zone, is probably in the University of Utah. Roewer, 1954: 1350; Bonnet, 1957: 2832.

Miagrammopes alboguttatus, — Banks, 1929: 89. (Not *M. alboguttatus* F. P.-Cambridge.)

I have examined the specimens identified as *M. alboguttatus* F. P.-Cambridge by Mr. Banks and am convinced that they are *M. simus*. Because the original description of the holotype female is so brief I have thought it worth while to offer a more detailed description of a selected female from the locality where I collected the original specimen and loaned it to the senior author. It is difficult to match males and females in this genus but I believe I have done so in this case. A male has also been selected and described in the following pages. Males and females are by far the most numerous of any species of the genus in my collection.

Female. Total length from anterior border of somewhat porrect chelicerae to posterior end of posterior spinnerets 6.63 mm. Carapace about 1.76 mm long; 1.41 mm wide at level of lateral ocular tubercles where it is widest; with a conspicuous pair of depressions slightly behind and somewhat medial to ME; with these depressions continued to the lateral margins by grooves in a slightly diagonal direction; with width only slightly narrowed to posterior margin; medial thoracic fovea short and slightly procurved. Eyes: four as usual, in a slightly procurved row, viewed from above; ratio of eyes ME : LE = 10 : 13; ME separated from one another by slightly less than nine times their diameter, from LE by about 1.6 times their diameter. Chelicerae: removal of these organs seems to show that the promargin of the fang groove has a single tooth and several minute cusps each with a stout, long hair; the retromargin of the fang groove appears to have a series of minute cusps each also with a stiff hair. Maxillae and lip: apparently quite typical of females of the genus (Fig. 37). Palpal tarsus with a robust claw having four or five very slender teeth (Fig. 38). Sternum: very angular; swollen near middle where a conspicuous shelf crosses from interval between second and third coxae; slopes sharply from high region both anteriorly and posteriorly; a second less conspicuous shelf crosses the sternum between third and fourth coxae; posterior end obscure but not extended between fourth coxae which are separated by about one-third of their width (Fig. 39). Legs: tibial index of first and fourth legs 10; all tarsi short; first tarsus slightly more than one-fifth as long as first metatarsus; all legs with fine hair; first tibia with a fringe of fairly long hair; apparently three true claws with several spurious claws on each tarsus; spines on fourth metatarsus and tarsus as shown in Figure 40; trichobothria appear to be present on femora, tibiae and metatarsi; the calamistrum extends over about seven-twelfths of length of fourth metatarsus; first leg nearly 3.5 times as long as third leg. Abdomen: essentially as shown in dorsal



Figures 37-44. *Miagrammopes simus* Chamberlin and Ivie. Fig. 37. Female maxillae and lip. Fig. 38. Female left palpal tarsus; prolateral view (with aid from dissected specimen). Fig. 39. Female sternum; seen from below. Fig. 40. Right fourth metatarsus and tarsus of female; retrolateral view. Fig. 41. Epigynum from below. Fig. 42. Carapace of male from above. Fig. 43. First tibia of male; retrolateral view (a few spines restored from scars). Fig. 44. Left palp of male; retrolateral view.

view in figure 11 of Chamberlin and Ivie, 1936; cribellum entire; spinnerets six as usual. Epigynum: somewhat obscured by hair; essential features shown in Figure 41 (variations in appearance have been noted among numerous specimens assigned to this species). Color in alcohol: legs generally brown with variations; first pair darkest of all but with tarsus light yellowish brown and metatarsus somewhat darker; carapace light yellowish brown throughout the dorsal region and with lateral sides dark brown; sternum yellowish brown with variations. Abdomen: with a semi-transparent cardiac area and white spotted area posterior to cardiac region; a pair of irregular, white stripes extend along the dorsum nearly the entire length; lateral regions brownish with an irregular white spot a little in front of the middle; venter light yellowish brown with some variation. Considerable variation in color pattern has been noted among the numerous specimens of this species now in the collection.

Male. Total length from anterior border of slightly porrect chelicerae to posterior end of abdomen about 3.05 mm (body curled and difficult to measure accurately). Carapace 1.06 mm long; 0.99 mm wide at level of lateral ocular tubercles; narrowed to 0.84 mm just behind ocular tubercles; pits and diagonal grooves, so conspicuous in the female, are here much less prominent; general appearance shown in Figure 42. Eyes: four as in female, in a straight row as seen from above; ME separated from one another by 8.5 times their diameter, from LE by about twice their diameter; ratio of eyes ME : LE = 7 : 10; lateral eyes directed somewhat ventrally. Chelicerae, maxillae and lip apparently as in female except for great reduction in size; details hidden by curled position and interlaced legs which are too fragile for disentanglement. Sternum: greatly swollen in middle but lacks the conspicuous transverse folds seen so clearly in the female; fourth coxae almost contiguous. Legs: tibial index of first leg 12, of fourth leg 11; calamistrum apparently lacking; first leg more than twice as long as second leg and nearly three times as long as third leg; first tibia with a battery of nearly two dozen robust spines on dorsal and dorsolateral sides essentially as shown in Figure 43; few spines observed elsewhere and the most conspicuous of these are on the first metatarsus. Palp: with femur, patella and tibia short and without special features; tarsus complicated and distinctive (Fig. 44). Abdomen: without noteworthy features; typical of males of the genus. Color in alcohol: in general light yellowish with variations; carapace with a somewhat angular, nearly white, central dorsal spot, with remainder of dorsum yellowish and with lateral sides grayish and with considerable black pigment in ocular region; sternum grayish; abdomen with dorsum light

yellowish with numerous white flecks; a broken, grayish stripe extends along each side of abdomen and the venter is irregularly grayish. Legs are yellowish in general but with variations; first legs with femora grayish retrolaterally; first tibiae, metatarsi and tarsi are all yellowish brown; other legs with grayish spots.

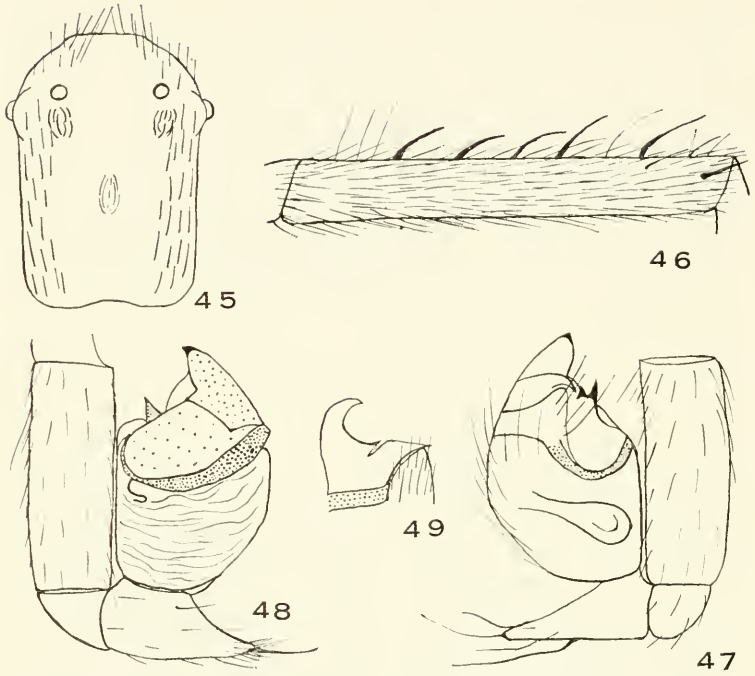
Records. Specimens assigned to this species have been collected on Barro Colorado Island, Panama Canal Zone, during each of my several periods of field work there beginning in 1934; I have a few records of the species from other localities in the Canal Zone and in Panama proper. The described female is from Barro Colorado Island, Canal Zone, May 18, 1964; the described male is from the same locality, August 2, 1954.

MIAGRAMMOPES TONATUS sp. nov.

Figures 45-49

Holotype. The male is from Jamaica, W. I., St. Andrew Parish, Mt. James at Plaintain River, October 24, 1957. The name of the species is an arbitrary combination of letters.

Description. Total length 3.45 mm. Carapace 1.08 mm long; 0.79 mm wide at level of lateral ocular tubercles; not conspicuously grooved as in some species in the genus; depressions just posterior to ME only moderately developed; median thoracic fovea only moderately depressed (Fig. 45). Eyes: four as usual, in a moderately recurved row, seen from above; ratio of eyes ME : LE = 5 : 6; ME separated from one another by about 6.5 times their diameter, from LE by slightly more than four times their diameter; lateral ocular tubercles only moderately developed. Chelicerae, maxillae and lip apparently quite typical of males of the genus. Sternum: with the usual form in this genus; greatly swollen, widened and extended between second and third coxae. Legs: tibial index of first leg 11, of fourth leg 8; calamistrum apparently lacking; first tibiae and metatarsi with few conspicuous, erect spines, others horizontal and hidden by hairs (Fig. 46); first leg more than twice as long as second leg, nearly twice as long as fourth leg and about three times as long as third leg; tarsal claws as usual; several trichobothria observed on tibiae and other segments. Palp: very short as usual; essential features shown in Figures 47-49. Abdomen apparently typical of males of the genus. Color in alcohol: carapace generally a dark gray with lighter spots and darker, irregular lines together with a dull, yellowish, ventral margin; sternum dark gray, lighter at anterior end; first pair of legs light yellowish brown ventrally, darker gray elsewhere except for tarsus which is yellowish brown;



Figures 45-49. *Miagrammopes tonatus* sp. nov. Fig. 45. Carapace of male from above. Fig. 46. First right tibia; retrolateral view. Figs. 47-48. Male palp; retrolateral and prolateral views, respectively. Fig. 49. Tip of tarsal bulb; nearly dorsal view.

legs 2-4 much as first but less conspicuously so; mouth parts yellowish with grayish streaks. Abdomen: with a somewhat indented, dark gray, median stripe extending from base for about three-fourths of length of abdomen and then joining a darker area which covers the posterior quarter of the dorsum; lateral to this median region are lighter areas with irregular, yellowish white spots; venter with a central, light, reticular stripe extending from genital groove to posterior end; on each side of this central stripe there is a narrow, irregular, semitransparent stripe and further laterally are reticulated areas; entire color pattern indefinite and difficult to describe adequately.

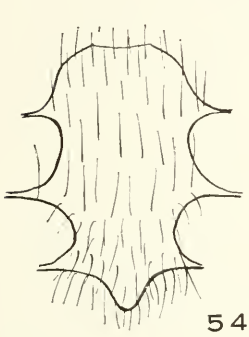
Records. An immature male taken with the holotype appears to belong to this species. The female is unknown.

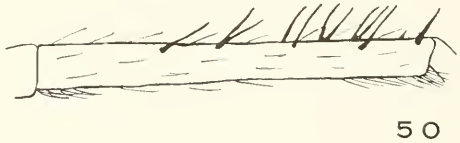
MIAGRAMMOPES UNIPUS sp. nov.

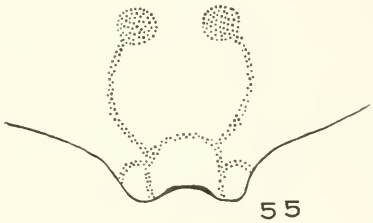
Figures 50-55

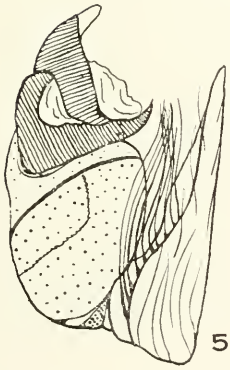
Holotype. The male is from Barro Colorado Island, Panama Canal Zone, June, 1950. The name of the species is an arbitrary combination of letters.

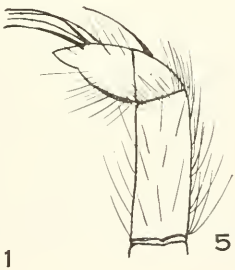
Description. Total length from anterior border of chelicerae to posterior end of spinnerets 3.58 mm. Carapace 1.06 mm long; 1.0 mm wide at level of lateral ocular tubercles; about 0.4 mm tall; with general form essentially as in *M. simus* Chamberlin and Ivie











Figures 50-55. *Miagrammopes unipus* sp. nov. Fig. 50. Right first tibia of male; retrolateral view. Figs. 51-52. Left palpal tarsus of male; prolateral and retrolateral views, respectively. Fig. 53. Left palpal femur, patella and tibia; retrolateral view (from male paratype). Fig. 54. Sternum of described female paratype; seen from below. Fig. 55. Epigynum; seen from below.

with depressions medial to ME moderately conspicuous but grooves leading to lateral border almost lacking. Eyes: four as usual, in a gently procurved row as seen from above; ME separated from one another by about eight times their diameter, from LE by slightly more than their diameter; ratio of eyes ME : LE = 8 : 10.5. Chelicerae: short and largely hidden by elongated maxillae which are twice as long as lip; all of these parts hidden by fragile surrounding structures. Sternum: elongated, narrow, quite convex opposite second coxae; continued laterally between second and third coxae; obtusely terminated between bases of fourth coxae but not continued between the latter, which are separated by about one-fifth of their width. Legs: tibial index of first leg 10, of fourth leg 7; first leg nearly three times as long as third leg; second leg only a little shorter than fourth leg; first tibia with a set of robust spines (Fig. 50); first metatarsus with fewer and less robust spines; tarsal claws as usual in the genus. Palp: distinctive features shown in Figures 51-53; femur of moderate length; patella and tibia extremely short. Abdomen: considerably flattened dorsally; otherwise typical of males of the genus. Color in alcohol: carapace with a narrow, central, somewhat broken grayish stripe; with considerable black pigment in ocular area; with a broad, lateral, grayish stripe on each side from lateral eyes to posterior border; the lower part of this gray stripe becomes lighter, thus adding another stripe to the lateral sides and, finally, the ventral margin is darker gray, thus making a total of seven distinguishable stripes on this part of the body; sternum yellowish with fairly broad, grayish margins. Abdomen: yellowish dorsally with two pairs of narrow, elongated, grayish spots dorsolateral in position and a series of small grayish spots at posterior end above spinnerets; laterally there are several short, grayish stripes; the venter has a narrow, median, grayish stripe with a narrow yellowish stripe on each side, and further laterally is a broader, light grayish stripe on each side; shortly in front of the reduced cribellum there is a narrow, grayish, transverse bar. Legs yellowish in general with several grayish spots and whole segments; fourth legs with most conspicuous grayish parts; fourth patellae dark gray; distal parts of fourth tibiae the same and nearly the entire metatarsi are gray.

Female paratype. The described female paratype measures 5.2 mm from anterior border of carapace to posterior end of spinnerets; length from anterior border of somewhat extended chelicerae to posterior end of spinnerets about 5.59 mm. Carapace 1.3 mm long; 1.32 mm wide at level of lateral ocular tubercles; medial to ME there is a fairly conspicuous depression in communication with a

narrow groove which extends along the border of the ocular tubercle to the lateral border of the carapace; another narrow groove in front of the ocular tubercle passes to the lateral border of the carapace and is connected to a short, narrow groove extending about half way through the tubercle between ME and LE; otherwise apparently typical of females of the genus. Chelicerae hidden and not clearly visible. Maxillae long, parallel, with rounded lateral borders. Lip: about three-fifths as long as maxillae; central portion swollen; sternal suture may not be a movable joint. Sternum: only moderately convex; not conspicuously swollen as in most females of the genus seen in this study; not extended between fourth coxae which are separated by nearly one-fourth of their width (Fig. 54). Legs: tibial index of first leg 10. of fourth leg 9; first leg twice as long as second leg and more than three times as long as third leg; fourth leg about 0.7 as long as first leg; spines appear to be lacking except for the moderately developed set of robust spines on fourth metatarsus and tarsus similar to those shown in Figure 40; legs with a fairly well developed coat of hair and first metatarsus has a moderately well developed ventral fringe; calamistrum appears typical of females of the genus. Abdomen: with a pronounced dorsal medial swelling; quite typical of females of the genus. Epigynum: obscure and difficult to observe clearly; observed essentials shown in Figure 55; a dorsal injury to the abdomen has permitted eggs to extrude, thus indicating that the female is nearly or quite mature. Color in alcohol: essentially as in male holotype except that the gray parts in that sex are here all considerably extended and blackened.

Records. The described female paratype was taken on Barro Colorado Island, Panama Canal Zone, August 22, 1939. Several male paratypes are in the collection from the type locality and taken as follows: August, 1936, 1950; July, 1939, 1950, 1954; February, 1958. One male paratype was taken at Summit, Panama Canal Zone, July, 1950. Three additional females are, with some uncertainty, placed in this species and were taken as follows: July, 1934; August, 1939; May, 1964, all from Barro Colorado Island, Canal Zone.

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GEOGRAPHIC VARIATION IN THE HISPANIOLAN FROG *ELEUTHERODACTYLUS WETMOREI* COCHRAN

Albert Schwartz[1]

Eleutherodactylus wetmorei Cochran is a brightly colored leptodactylid frog which was described from a series of four specimens collected by Dr. Alexander Wetmore at Fond des Nègres, Département du Sud, Haiti. The holotype and paratypes were taken from a communal nest of the Palm Chat (*Dulus dominicus* Linnaeus) along with two *Hyla dominicensis* Tschudi (Cochran, 1932:191). Later, Cochran (1941:76-77) reported 11 additional specimens of *E. wetmorei,* collected by W. L. Abbott, from Moron, Département du Sud, Haiti, near the extreme western tip of the Tiburon Peninsula. Both the typical and Abbott specimens were especially poorly preserved, but the frog is a very distinctive one in pattern (and in coloration in life). Two populations of *E. wetmorei* have the concealed surfaces of the hindlimbs with dark patterns on the brightly colored (orange to yellow) ground color; Cochran pointed out, however, that the Moron frogs seemed to lack this distinctive thigh pattern, and Shreve and Williams (1963:324) commented that two of the Moron series they examined lacked thigh markings, in contrast to the single individual they had from the Pétionville area.

The two-note voice of *E. wetmorei* is prominent in nocturnal choruses throughout southern Haiti; the frogs, however, are arboreal (as the situation for the type series intimates), and collecting series of *E. wetmorei* is extremely difficult. Through the efforts of Dr. Ernest E. Williams, several excellent lots of *E. wetmorei* are now available from some Haitian localities, including the southern slope of the Massif de la Selle in the vicinity of Thiotte, and from the area between Jérémie and Dame-Marie at the extreme tip of the Tiburon Peninsula. The latter specimens amply confirm the

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distinctness of the distal peninsular population of *E. wetmorei,* and the Thiotte specimens likewise demonstrate characters (which also occur elsewhere along the Dominico-Haitian border) distinctive to the populations in that region. Remarkably, there is now more material of these two peripheral populations than there is of the nominate subspecies, although I have taken specimens of the latter at Camp Perrin on the southern foothills of the Massif de la Hotte. Aside from my own material in the Albert Schwartz Field Series (ASFS), I have examined specimens in the American Museum of Natural History (AMNH), Carnegie Museum (CM), Museum of Comparative Zoology (MCZ), and United States National Museum (USNM); for the loan of these frogs I am grateful to Charles M. Bogert and George W. Foley, Neil D. Richmond and Clarence J. McCoy, Jr., Ernest E. Williams, and Doris M. Cochran. In the field I have had the capable assistance of Ronald F. Klinikowski, David C. Leber, and Richard Thomas. Messrs. Leber and Thomas were successful in securing the first specimen of *E. wetmorei* from the República Dominicana; it was this frog, strikingly different from material I had seen in life at Camp Perrin, which prompted the present study. The excellence of the illustrations is once more due to the work of Mr. Leber.

The collections in Haiti made for the Museum of Comparative Zoology were financed by NSF Grant 16066 to Dr. Ernest E. Williams.

SYSTEMATIC ACCOUNTS

ELEUTHERODACTYLUS WETMOREI Cochran, 1932

Eleutherodactylus wetmorei Cochran, 1932, Proc. Biol. Soc. Washington, 45: 191.

Eleutherodactylus auriculatus wetmorei, — Cochran, 1941, Bull. U. S. Natl. Mus., 177:74.

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Remarks: Although *E. wetmorei* was originally named as a distinct species, Cochran later (1941:75) considered *wetmorei* closely related to *E. auriculatus* Cope (= *E. varians* Gundlach and Peters). Later still, I (Schwartz, 1960:6) suggested that *wetmorei* might indeed be correctly regarded as a subspecies of *E. varians,* since the two forms have several structural and pattern features in common (although chromatically they differ strikingly). The

calls of *E. varians* and *E. wetmorei* are, however, very different (Schwartz, in press), the call of *E. wetmorei* resembling that of the Cuban *E. eileenae* Dunn rather than *E. varians*. Accordingly, I have once more separated *E. wetmorei* nomenclatorially from *E. varians;* the former species is limited to Hispaniola, the latter to Cuba and the Isla de Pinos.

Eleutherodactylus wetmorei wetmorei Cochran

Type locality: Fond des Nègres, Dépt. du Sud, Haiti; holotype, USNM 72617.

Definition: A subspecies of *E. wetmorei* characterized by anterior and posterior faces of thighs reticulate black to dark brown on an orange ground, and groin orange with similarly colored reticulum (Fig. 2A).

Remarks: There are only ten specimens which I assign to the nominate subspecies; of these, the two paratypes (USNM 72618-19) are in extremely poor condition, and three (ASFS X2993-95) are juveniles with snout-vent lengths between 11.5 and 18.2 (all measurements in millimeters). Mensural data for a single male (ASFS X2684) are: snout-vent length 28.7, head length 11.3, head width 12.8, tympanum 2.0, eye 4.0, naris to eye 3.8, femur 12.8, tibia 15.2, fourth toe 11.5; measurements of four females (extremes and means) are: snout-vent length 33.5-35.1 (34.2); head length 12.0-13.5 (12.9); head width 13.3-14.7 (14.1); tympanum 2.2-2.5 (2.3); eye 3.8-4.8 (4.2); naris to eye 3.7-4.5 (4.2); femur 14.1-15.2 (14.8); tibia 17.1-17.8 (17.4); fourth toe 13.4-14.3 (13.8).

The condition of the topotypes of *E. w. wetmorei* precludes absolute assurance that the material from Camp Perrin is identical in pattern to them. Cochran's figure (1941:75, fig. 24) however, shows quite clearly that the anterior and posterior faces of the thigh are darkly reticulate, and these markings plus the pale interocular bar are still barely visible on the holotype. Although Fond des Nègres lies in the extreme northeastern foothills of the Massif de la Hotte and Camp Perrin lies in the southwestern foothills of the same range, the Camp Perrin specimens agree fairly closely in thigh design with the Fond des Nègres material. Accordingly I consider the Camp Perrin specimens to be *E. w. wetmorei,* although there is a possibility that, with the acquisition of fresh topotypical material, the Camp Perrin population will be found to differ from that at Fond des Nègres.

Fresh specimens of *E. w. wetmorei* from Camp Perrin are tan to brownish tan in life, with a very faint pair of dorsolateral pale lines (ASFS X2684) present in one individual. The posterior and anterior faces of the thigh, the groin, and the upper surface of the pes were orange (pl. 2 D 12; all color designations from Maerz and Paul, 1950) in life, and the entire ventral surface was yellow (pl. 9 L 5). Both faces of the thighs, as well as the groin, are overlaid with a dark brown to greenish black reticulum; reticulum remnants more or less outline the orange groin patch and separate the bright color from the more drab dorsal tan. The sides are at times vaguely marked with a brown reticulum which extends, in a diluted fashion, onto the chest as an area of brownish dots or flecks. The throat may be flecked with brown, and there is a pair of yellow-orange glands on the posterior portion of the throat; inguinal glands are absent in the species. The underside of the hindlimbs is usually marked with brown continuations of the anterior and posterior thigh pattern, and the crus also shows some ventral brown reticulations. The ventral crural reticulum is a continuation of the anterior and posterior crural reticulum, occupying the concealed surfaces of the crus. All specimens have a pale (tan to buffy) broad interocular bar, with one exception (MCZ 35199) which now appears to lack this feature. In the juveniles, the entire thigh was yellow in life, but the thigh pattern is identical to that of adults. In adults, the iris is golden above and below, whereas in juveniles the iris is metallic buffy.

At Camp Perrin, *E. w. wetmorei* was abundant in trees about the settlement, and the ringing two-note call made up a prominent portion of each night's choruses. Specimens, on the other hand, were difficult to secure; the three juveniles were taken by Mr. Leber from arboreal bromeliads, whereas the adult male (ASFS V2684) was obtained while calling on a *Sansevieria* leaf only one foot off the ground. Like the equally arboreal Cuban *E. varians, E. wetmorei* occasionally can be collected when it calls from low vocalizing sites.

As pointed out above, all known localities for *E. w. wetmorei* are associated with the lower slopes of the Massif de la Hotte. The locality near Miragoâne is unlocatable on any current map, so it is possible that this specimen came from a lower elevation than the other *E. w. wetmorei;* the elevation at Camp Perrin is 1000 feet (305 meters) and that at Fond des Nègres is 730 feet (240 meters). Figure 1 shows localities for specimens of *E. w. wetmorei.*

Specimens examined: Haiti, Dépt. du Sud, Camp Perrin, 6 (ASFS X2684, X2897, X2962, X2993-95); Fond des Nègres, 3 (USNM 72617 — holotype; USNM 72618-19 — paratypes); Butête, nr. Miragoâne, 1 (MCZ 35199).

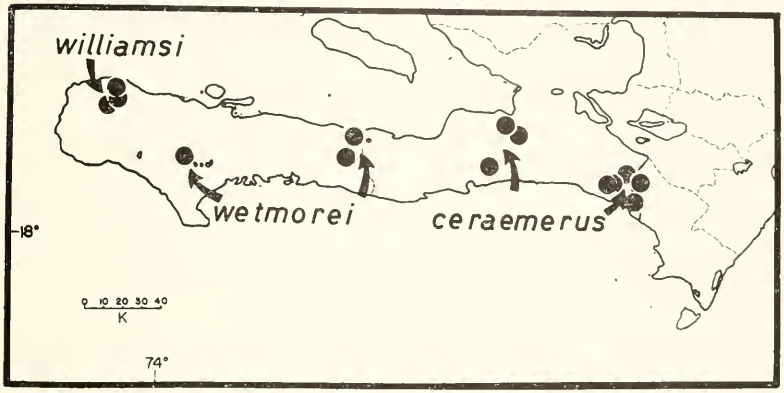

Fig. 1. Map of southwestern Haiti, showing the Tiburon Peninsula. Localities for *E. wetmorei wetmorei, E. w. williamsi,* and *E. w. ceraemerus* are shown as solid circles.

Eleutherodactylus wetmorei ceraemerus
new subspecies

Holotype: MCZ 36101, an adult female, from Thiotte, Dépt. de l'Ouest, Haiti, one of a series collected April 1962 by G. Whiteman.

Paratypes: MCZ 36097-100, 36102-05, USNM 146614, same data as holotype; MCZ 37216-18, same locality as holotype, summer 1962, G. Whiteman; CM 38550-55, same locality as holotype, June 1962, G. Whiteman; MCZ 36107-11, Tête à l'Eau, near Saltrou, Dépt. de l'Ouest, Haiti, April 1962, G. Whiteman; CM 37786, MCZ 34501, Marbial, 21 km NE Jacmel, Dépt. de l'Ouest, Haiti, 20-21 April 1961, L. Whiteman; AMNH 44034, ridge of Massif de la Selle, just south of Savane Zombi, on Saltrou road, "4500 feet," Dépt. de l'Ouest, Haiti, 6 April 1935, W. G. Hassler; MCZ 34503, AMNH 44050, Colombia (= Colombier), Dépt. de l'Ouest, Haiti, 6 April 1935, W. G. Hassler; MCZ 34502, AMNH 44036-37, La Mahot, near Colombia (= Colombier), Dépt. de l'Ouest, Haiti, 7 April 1935, W. G. Hassler; MCZ 31733, Boutillier Road, Dépt. de l'Ouest, Haiti, 9 August 1959, E. E. Williams

and A. S. Rand; MCZ 37141, La Boule, Dépt. de l'Ouest, Haiti, 18 April 1960, J. A. Rivero; ASFS V2711, 7 km SE Los Arroyos, 2200 feet (720 meters), Pedernales Province, República Dominicana, 29 June 1964, R. Thomas.

Definition: A subspecies of *E. wetmorei* characterized by anterior and posterior faces of thigh bright orange with a pattern of black spots rather than a reticulum, and groin orange with scattered black dots and outlined by black (Fig. 2B).

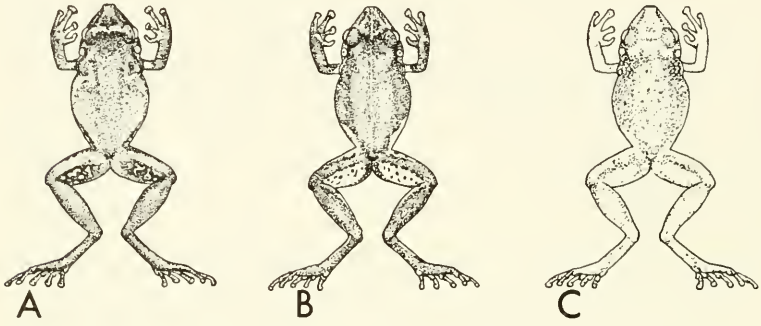

Fig. 2 Three subspecies of *E. wetmorei,* as follows: A, *E. w. wetmorei,* ASFS X2962, Camp Perrin, Dépt. du Sud, Haiti; B, *E. w. ceraemerus,* MCZ 36101, holotype, Thiotte, Dépt. de l'Ouest, Haiti; C, *E. w. williamsi,* MCZ 37757, holotype, Marfranc, Dépt. du Sud, Haiti.

Description of holotype: An adult female with the following measurements: snout-vent length 35.6, head length 12.7, head width 14.5, longitudinal diameter of tympanum 2.5, longitudinal diameter of eye 4.5, naris to eye 4.0, femur 14.7, tibia 17.5, fourth toe 13.8. Head distinctly broader than long; snout truncate, with nares conspicuous at anterior end of canthus rostralis; diameter of eye slightly longer than distance from naris to anterior corner of eye; diameter of tympanum much less than diameter of eye, distance from tympanum to eye slightly less than diameter of tympanum. Interorbital distance 5.4, greater than diameter of eye. Digital discs present, large, those on digits 2, 3, and 4 only slightly smaller than area of tympanum. Fingers short, basally with a very small web, 3-4-2-1 in order of decreasing length; subarticular tubercles pale, concolor with palmar surface of hand. Toes moderately long, only very slightly webbed basally, 4-3-5-2-1 in order of decreasing length; subarticular tubercles prominent, concolor with plantar surface. Heels overlap strongly when femora are held at

right angles to body axis. Inguinal glands absent. Dorsum smooth. Throat and chest smooth, belly coarsely granular. Dorsal surface of fore- and hindlimbs smooth. Posterior and ventral faces of thighs covered with moderately sized juxtaposed flattened granules. Tongue large, free and notched behind, its greatest width equal to about two-thirds of that of floor of mouth. Vomerine teeth in two small, almost diagonal patches, enclosed within the median margins of the choanae, separated from them by a distance equal to the diameter of a choana, the two patches separated medially by a distance equal to about half the length of a single vomerine patch.

Coloration and pattern of holotype: Dorsum (as preserved) brown and without pattern except for a vaguely discernible paler interocular bar and a very faint middorsal hairline; hindlimbs concolor with dorsum; concealed surfaces of thigh, crus, and pes paler (presumably orange in life) with scattered dark brown dots and outlined with a faintly darker brown line, punctate with dark brown dots along its length; groin spot pale (presumably orange in life) with a few scattered dark dots on the left side (right side immaculate), the groin spot outlined by a vague darker line and sharply set off from the dorsal color; forelimbs dark brown, concolor with the dorsum but with a sharply distinct pale mark on the wrist and another at the forelimb insertion. Venter pale (presumably orange in life), heavily suffused with brown stippling on the sides anteriorly (anterior to the pale groin spot); throat densely stippled with dark brown; underside of forelimbs dark brown on antebrachium, pale on brachium. A pair of moderately prominent glandular areas on the posterior throat anterior to the level of the forelimb insertions.

Variation: The series of nine male *E. w. ceraemerus* has the following measurements (extremes and means): snout-vent length 28.5-33.4 (30.4), head length 9.8-11.8 (10.8), head width 10.8-12.6 (12.2), tympanum 1.7-2.0 (1.8), eye 3.4-4.0 (3.7), naris to eye 2.9-3.9 (3.5), femur 11.6-14.2 (13.2), tibia 14.5-15.9 (15.2), fourth toe 11.2-12.3 (11.7). Twenty females have the following measurements: snout-vent length 26.7-38.3 (34.4), head length 9.6-13.3 (11.9), head width 10.8-15.0 (13.5), tympanum 1.6-2.5 (2.1), eye 3.1-4.7 (4.1), naris to eye 3.2-4.5 (3.8), femur 11.9-16.8 (14.6), tibia 14.1-18.9 (17.2), fourth toe 10.4-14.3 (13.2).

As preserved, the paratypes agree well in color with the holotype, although some specimens are paler (tan rather than brown). In coloration, the concealed hindlimb surfaces and the groin spot are always sharply and conspicuously set off from the remainder of the hindlimb, and the pattern of these areas is regularly one of dots or

spots, never a reticulum as in *E. w. wetmorei.* At times the spots or dots are somewhat fused (MCZ 34501), but the condition never approaches that of the nominate subspecies. The groin spot may have some dark flecking within it, or it may be immaculate; in either case it is outlined dorsally by a dark and punctate line as in the holotype. Some specimens show a pale interocular bar (MCZ 36105), but this is not the regular condition in *ceraemerus.* A very fine median hairline is barely discernible in some specimens (USNM 146614), as it is in the holotype, but most frogs lack this pattern element. Other specimens (MCZ 36102) have some fine and vague stippling along the lower sides above the venter, but this condition likewise occurs only sporadically. Only those frogs which are dorsally as dark as the holotype have the sides of the venter anterior to the groin spot as darkly pigmented as does the holotype.

There are only two specimens from north of the Massif de la Selle, those from La Boule and Boutillier Road; the balance of the series is from the southern side of that massif. I do not know if the ranges of these two populations are continuously directly across the massif, but it does not seem likely, since my impression is that *E. wetmorei* is generally a frog of low to moderate elevations in forested situations. In any event, the two frogs from north of the La Selle agree in thigh pattern details with those from the southern slope except that the degree of fusion between the spots is greater than is customary for southern specimens. It seems quite likely that another subspecies will be found to inhabit the northern slopes of the La Selle and its associated ranges above Port-au-Prince; the thigh pattern of these northern specimens does not approach the reticulum of *E. w. wetmorei.*

Structurally, the paratypes agree with the holotype except that the buccal cavity of the latter is somewhat aberrant. In most specimens of *E. w. ceraemerus,* the vomerine patches are small, compact, and enclosed well within the inner margins of the choanae, separated from the choanae by a distance equal to that of one vomerine series and separated from each other by a similar distance. In the holotype, the vomerine patches are closer to one another than in the balance of the series.

Comparisons: Comparison of the subspecies *wetmorei* and *ceraemerus* is hardly necessary; the two forms can be easily distinguished by the pattern of the concealed surfaces — reticulate in *wetmorei,* dotted in *ceraemerus.* Size differences are difficult to assess, since the series of *E. w. wetmorei* is very small. *E. w. ceraemerus* seems the larger of the two forms.

Although there are no color data on most specimens of *E. w. ceraemerus,* Richard Thomas recorded the color in life of the Dominican specimen as follows: dorsum grayish tan (= putty colored), venter bright orange. Forearm insertions, pre- and postfemoral surfaces, and groin bright orange with black dotting. Undersides of legs and dorsal and ventral surfaces of feet bright orange; dark flecking roughly outlining region of contact between orange and tan on both limbs and groin.

Remarks: The abundance of specimens of *E. w. ceraemerus,* in contrast to the paucity of those of the nominate subspecies, is puzzling, although it is possible that the frog is more abundant or more easily secured on the southern slope of the Massif de la Selle than it is farther west. The Dominican specimen was collected while it was calling about ten feet above the ground in a coffee tree; others were heard calling in the same general region, but most were vocalizing high in the trees and thus were inaccessible. The scarcity of specimens from the Morne l'Hôpital above Pétionville is equally puzzling; the calls of this frog were commonly heard between Pétionville and Fermate, but there are only two specimens from this entire region. The species apparently is absent from the Sierra de Baoruco, where the dominant, moderately sized, more or less arboreal *Eleutherodactylus* is *E. armstrongi* Noble and Hassler. This species also occurs south of Port-au-Prince on the Montagnes Noires at Furcy, an area where *E. wetmorei* is absent. The Dominican specimen is from the extreme edge of the República Dominicana in what may well be considered the eastern extreme of the Massif de la Selle.

The altitudinal limits of *E. w. ceraemerus* vary from a low elevation of about 600 feet (200 meters) at Marbial to high elevations of about 4270 feet (1400 meters) near Savane Zombi. These elevations are greater than those of the nominate subspecies to the west. The name *ceraemerus* is derived from the Greek "keraia," a dot, and "meros," thigh, an illusion to the dotted concealed surfaces of the hindlimbs in this subspecies.

Eleutherodactylus wetmorei williamsi new subspecies

Holotype: MCZ 37757, an adult female, from Marfranc, Dépt. du Sud, Haiti, one of a series collected 26-27 December 1962 by Hill and Vuilleumier.

Paratypes: MCZ 37751-56, 37758-63, same data as holotype; MCZ 37587, Perine, near Jérémie, Dépt. du Sud, Haiti, December 1962, G. Whiteman; MCZ 37586, Carrefour Sanon, near Jérémie,

Dépt. du Sud, Haiti, December 1961, G. Whiteman; USNM 60627-35, Moron, Dépt. du Sud, Haiti, 20 December 1917, W. L. Abbott. MCZ 28599-600, Moron, Dépt. du Sud, Haiti, 24 December 1917, W. L. Abbott.

Definition: A subspecies of *E. wetmorei* characterized by complete absence of pattern on anterior and posterior faces of thigh and on groin spot (Fig. 2C).

Description of holotype: An adult female with the following measurements: snout-vent length 33.8, head length 11.8, head width 13.0, longitudinal diameter of tympanum 2.0, longitudinal diameter of eye 4.2, naris to eye 4.1, femur 14.2, tibia 16.9, fourth toe 13.1. Head distinctly broader than long; snout truncate, with nares conspicuous at anterior end of canthus rostralis; diameter of eye about equal to distance between naris and anterior corner of eye; diameter of tympanum much less than diameter of eye, distance from tympanum to eye equal to about one-half the diameter of tympanum. Interorbital distance 4.0, slightly less than diameter of eye. Digital discs present, large, those on digits 2, 3, and 4 only slightly smaller than area of tympanum. Fingers short, basally with a very small web, 3-4-2-1 in order of decreasing length; subarticular tubercles pale, concolor with palmar surface of hand. Toes moderately long, only very slightly webbed basally, 4-3-5-2-1 in order of decreasing length; subarticular tubercles prominent, concolor with plantar surface. Heels overlap strongly when femora held at right angles to body axis. Inguinal glands absent. Dorsum smooth. Throat and chest smooth, belly coarsely granular. Dorsal surface of fore- and hindlimbs smooth. Posterior and ventral faces of thighs covered with moderately sized, juxtaposed, flattened granules. Tongue elongate and narrow, free and notched behind, its greatest width equal to about one-half of that of floor of mouth. Vomerine teeth in two very small patches, well enclosed within the median margins of the choanae, separated from them by a distance equal to the length of one vomerine series, the two patches separated by a distance equal to the length of one vomerine patch.

Coloration and pattern of holotype: Dorsum (as preserved) pale tan, heavily stippled with brown on the trunk; head less densely stippled and with remnants of a pale interocular bar, outlined anteriorly and posteriorly by remnants of brown lines; upper surfaces of hindlimbs concolor with dorsum; concealed surfaces of thigh, crus and pes paler (presumably brightly colored in life) without any dark markings or outlining in darker; groin spot also paler and without dark markings or outlining; forelimbs tan, concolor with dorsum. Venter pale (presumably brightly colored in life), without

heavy stippling; throat unstippled but with a pair of darker glandular areas anterior to the forelimb insertions.

Variation: The single male *E. w. williamsi* has the following measurements: snout-vent length 32.7, head length 11.5, head width 13.1, tympanum 1.6, eye 4.0, naris to eye 3.9, femur 14.6, tibia 16.4, fourth toe 12.9; the series of 21 females has the following mensural data (extremes and means): snout-vent length 25.2-36.4 (32.7), head length 9.5-12.2 (11.5), head width 10.7-14.0 (13.1), tympanum 1.2-2.3 (1.8), eye 3.0-4.7 (3.9), naris to eye 3.1-4.5 (3.5), femur 11.2-15.2 (13.5), tibia 14.0-18.0 (15.7), fourth toe 9.1-14.0 (11.9).

The paratypic series includes both long-preserved and freshly collected material; the former is the lot from Moron and the latter material is from the type locality and from near Jérémie. Many recent specimens have the more or less speckled dorsal aspect of the type, but this style of pattern does not occur in the Moron material, a fact which I assume is due to the length of time in preservation. The presence of the interocular bar is variable, but it is demonstrated in both old and new specimens; many frogs show this feature more diagrammatically than does the holotype. A median dorsal hairline occurs in some individuals (MCZ 37759, USNM 60629). There is never any indication of dark pattern on the concealed surfaces nor in the groin, these areas being quite pale; the freshly taken specimens still show a weak pinkish-orange wash on the thigh, so that I assume that these areas were quite brightly colored in life, presumably some shade of yellow or orange like the two other subspecies of *E. wetmorei*. Structurally, the paratypes agree very closely with the description of the holotype.

Comparisons: E. w. williamsi is easily distinguished from the nominate subspecies and *E. w. ceraemerus* since it lacks any indication of thigh or groin pattern. As preserved, the specimens of *williamsi* are regularly paler than those of the other subspecies, and it seems possible that there is a dorsal chromatic difference between *williamsi* and the other subspecies. *E. w. williamsi* does not appear to reach so large a size as does *ceraemerus* but exceeds slightly the maximum size recorded for *E. w. wetmorei*. The absence of detailed color data in life for *E. w. williamsi* hampers more detailed comparisons.

Remarks: E. w. williamsi occupies the extreme northwestern portion of the Tiburon Peninsula in Haiti. Its range, as now known, is circumscribed, with all localities being associated with the Monts Cartaches to the west of Jérémie. Altitudinally, *E. w. williamsi*

occurs somewhat lower than the two more eastern subspecies, from a low elevation of about 130 feet (40 meters) at Moron to 1440 feet (440 meters) at Carrefour Sanon; Perine is not locatable.

The distinct patternless condition of the western population was first recognized by Cochran (1941:76), who pointed out that the series from Moron was light in color; later, Shreve and Williams (1963:324) again commented that the Moron series lacked limb and groin markings, in contrast to their specimen from Boutillier Road (*ceraemerus*). The new series in the Harvard collection amply confirms these differences and demonstrates that they are not due to fading or the age of the previously known material from this region. I take great pleasure in naming the far western subspecies of *E. wetmorei* for Dr. Ernest E. Williams, whose interest in Hispaniolan herpetology, sponsorship of field work on that Antillean island, and generous cooperation with others involved with Hispaniolan herpetological problems can be acknowledged only in a token fashion by the use of his name as a patronymic designation for this distinctive subspecies.

DISCUSSION

E. wetmorei is now known to be widely distributed along the length of the Tiburon Peninsula in Haiti; the altitudinal limits of the species indicate that it is an inhabitant of low to moderate elevations associated with the north and south flanks of the massifs de La Selle and de La Hotte. There is but one record from the República Dominicana, along the Dominico-Haitian border in the extreme eastern ranges of the Massif de La Selle. The species remains unknown from the Sierra de Baoruco proper. Doubtless many areas in Haiti whence *E. wetmorei* remains unknown will ultimately be found to be inhabited by this species; since the frog is predominantly arboreal, it is difficult to collect, and often the species has been heard vocalizing in areas where specimens were impossible to secure.

As in several other south island (*sensu* Williams, 1961) amphibians and reptiles, *E. wetmorei* has differentiated into a series of three distinct populations which are easily recognizable. Although there is really too little material to be certain, it is interesting that the specimens from Fond des Nègres agree with those from Camp Perrin on the southern slopes of the Massif de La Hotte farther to the west. Such a similarity is remarkably like that shown in *Sphaerodactylus copei* Steindachner, wherein material from the vicinity of Miragoâne (and thus near the Fond des Nègres) is like

S. c. cataplexis Schwartz and Thomas (at Camp Perrin) rather than like *S. c. picturatus* Garman (at Jérémie). Apparently the low and forested pass across the Massif de La Hotte in the Aquin-Fond des Nègres-Miragoâne region has allowed passage of some southern subspecies to the north coast, thereby more or less separating the two north coast populations (*S. c. picturatus* and *S. c. copei* separated by *S. c. cataplexis,* just as *E. w. williamsi* and *E. w. ceraemerus* are separated by *E. w. wetmorei;* see Schwartz and Thomas, 1965, for details of gecko distributions in this region). Such similarities seem hardly due to chance.

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A NEW SPECIES OF TRIBOLONOTUS (LACERTILIA: SCINCIDAE) FROM BOUGAINVILLE AND BUKA, SOLOMON ISLANDS, WITH COMMENTS ON THE BIOLOGY OF THE GENUS

Allen E. Greer and Fred Parker[1]

INTRODUCTION

The skinks of the genus *Tribolonotus* are undoubtedly one of the most bizzare taxa of lizards. Indeed, many of their anatomical features such as abdominal glands (Parker, 1940), volar pores (Roux, 1930 and 1934; Parker, 1940), and single right functional oviduct (discussed below) are as yet unreported in other lizards. Among skinks, these features, as well as their anomalous head and body squamation, make them one of the most easily distinguished groups in an otherwise taxonomically difficult family.

In this paper we describe an unnamed species of the genus and discuss various aspects of the ecology, reproductive biology, and behavior of several species.

DESCRIPTION OF A NEW SPECIES OF *TRIBOLONOTUS*

During a recent period of residence (1962-1963) on Bougainville Island and a subsequent return trip (1966) to the northern Solomons, Parker collected a large number of specimens of a hitherto unnamed species of *Tribolonotus* on the islands of Bougainville and Buka. The new species is very similar in many details of squamation to *T. ponceleti* Kinghorn, 1937, which occurs on Bougainville and Shortland islands, and may therefore be known as

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TRIBOLONOTUS PSEUDOPONCELETI[1] new species

Holotype: Museum of Comparative Zoology (MCZ) 72914, an adult male collected by Fred Parker at Kunua, Bougainville, on 30 December 1962.

Paratypes (610 specimens): BOUGAINVILLE: KUNUA: MCZ 72767-72779, 72781-72785, 72790-72791, 72793-72805, 72807-72813, 72815-72829, 72831-72863, 72865-72866, 72868-72869, 72871-72873, 72875-72900, 72910-72912, 76148, 76155-76178, 76181-76191, 76193-76201, 76412-76469, 78094-78282, + 4 untagged specimens; American Museum of Natural History (AMNH) 92026-92058, + 10 untagged specimens; Australian Museum (AM) R 26603-26607; British Museum (BM) 1963.578-1963.584; Field Museum of Natural History (FMNH) 141982-141985, 152596; University of Kansas Natural History Museum (UKNHM) 98510-98511; Zoological Museum of Berlin (ZMB) 39155 (2 specimens). BOKU: MCZ 65878-65880, 67723-67726; AMNH 89433. KIETA: MCZ 65875-65877, 67249-67250. MATSIOGU area: MCZ 92423-92426, 92428, 92468, 92492-92495. MELILUP: MCZ 92429-92433. MUTAHI: MCZ 87615-87623, 88782-88794, 91467-91472, 92394-92422, 92427, 92434-92440. Above POPHEIARAI: MCZ 76179. RAMAZON RIVER (1600-2400 feet): MCZ 92502-92503.

BUKA ISLAND: MCZ 67706-67716, 73850-73861; AMNH 89434. KUBA: MCZ 92491.

Diagnosis: Pseudoponceleti differs from *blanchardi* of the Solomons in having two rows of enlarged vertebral scales instead of a single row as in *blanchardi*. *Schmidti* of the Solomons also has two rows of enlarged vertebral scales, but whereas these scales extend anteriorly to the single large parietal scale in *schmidti*, they only extend to a point just anterior to the level of the insertion of the forelegs in *pseudoponceleti*. Size is the easiest way to distinguish *ponceleti* from *pseudoponceleti*. The three specimens of

[1] The similarity in certain points of squamation between *T. ponceleti* and the new species, as well as their supposed sympatry (but see Ecology section of paper below), has caused the new species to be confused with *ponceleti* both in the field and in museum collections. Fortunately, this confusion has been carried over into the literature only once (Zweifel, 1966). To help clarify the taxonomic confusion, it seems best to take the path of least nomenclatural confusion and call the new species *pseudoponceleti*.

ponceleti known in collections range from 116-125 mm in snout-vent length, whereas the largest of 611 *pseudoponceleti* examined is only 73 mm in snout-vent length.

Gracilis and *novaeguineae* of New Guinea can be immediately distinguished from *pseudoponceleti* by means of the greatly enlarged spines on the two vertebral and paravertebral scale rows, and the head casque which, posteriorly, is raised above the level of the nape.

Pseudoponceleti differs from *annectens* of New Britain (known from the holotype and more recently from a second specimen in the Zoologisk Museum, Copenhagen[1]) in several scale characters which are summarized here from Zweifel (1966; see Fig. 1). "In both species there is a prominent row of enlarged scales paralleling the much larger vertebrals, but where at midbody in *pseudoponceleti* there is one of these smaller scales for each vertebral, *annectens* has only one for every two vertebrals. There are two primary temporal scales in *pseudoponceleti* and three in *annectens*." The first infralabial in *pseudoponceleti* is long and thin and extends posteriorly almost to exclude the second infralabial from the edge of the lip, or in a very few cases (1 specimen in 46 examined by Zweifel, 1966) the first labial does just exclude the entire second infralabial from the edge of the lip. In *annectens* the first infralabial extends posteriorly to exclude the second (in the type) or the second and third (in the Copenhagen specimen) infralabials from the edge of the lip.[2]

Description (Fig. 2; also see fig. 1 in Zweifel, 1966): *T. pseudoponceleti* measures between 26 and 73 mm in snout-vent length, with the tail approximately 59 to 65 per cent of the total length. The pentadactyl limbs are well developed and overlap when adpressed to the body. The head is deep and rather triangular in shape when viewed from above. The longitudinal striations on the head, the keeled vertebral and caudal scales, and the enlarged scales on the sides and limbs give the animal a rather rugose appearance.

[1] The locality data for this second known specimen of *annectens* are as follows: Yalom, 35 km S.E. of Cape Lambert, Gazelle Peninsula, New Britain. Elevation 1000 meters above sea level.

[2] As these infralabials are excluded from the edge of the lip, they might be called sublabials as Zweifel (1966) notes. We choose to call them infralabials here, however, to emphasize the proper homologous relationships.

The rostral is approximately 2½ times as wide as deep. A very large frontonasal covers the dorsal surface of the snout, and prefrontals are absent. The frontal is slightly shorter than the frontonasal and touches this scale throughout its entire anterior length. The frontal is in contact with the 2 anterior supraoculars laterally and the frontoparietals posteriorly. There are 4 supraoculars. The frontoparietals are distinct or fused to varying degrees. A distinct interparietal is lacking. The single large parietal, within which lies the parietal eye, is bounded on both sides by a smaller anterior and posterior parietal scale.[1]

The nostril is contained in a single nasal. A large, roughly rectangular loreal extends from the anterior corner of the eye to the nasal and first supralabial. There are 5 supralabials; the first is extremely long and thin and extends posteriorly to the level of the anterior half of the eye, thereby excluding the anterior 2/5 of the large, rectangular second supralabial from the margin of the lip. A large 3rd and smaller 4th and 5th supralabial follow. Both the second and third supralabials border the smaller scales of the entirely scaly eyelid. There is a small scale above the 4th supralabial and two superposed scales are above the 5th supralabial. Posterior to these last 3 scales are the two temporal scales, of which the lower is about twice the size of the upper.

The mental is followed on either side by 5 or 6 infralabials. The first of these is long and thin and extends posteriorly about as far as does the first supralabial above. The first infralabial excludes approximately ½-¾ of the second infralabial from the margin of the lip. A single large postmental is followed by a pair of very large chin scales which form a suture along the midline and are followed by a second part of chin scales of slightly smaller size. These chin scales are separated by 4 of the smaller gular scales.

All the large head scales bear longitudinal ridges or keels.

The tympanum is almost level with the surface of the head. Auricular lobes are lacking.

[1] Zweifel's (1966) interpretation of the single large median parietal as possibly resulting from the fusion of the interparietal and parietals seems perfectly plausible to us. In all other lygosomine skinks the parietal eye occurs in an interparietal which would argue for the interparietal's being part of the single median parietal of *Tribolonotus*. Zweifel's observation of the incomplete posterior median suture in the large parietal can certainly be seen in many *pseudoponceleti* and again argues for the paired lygosomine parietals having become part of the single shield.

There are 21-26 pairs of enlarged, keeled, vertebral scales between the base of the tail and a point just anterior to the insertion of the forelimbs. Between each of these pairs of enlarged vertebrals there is usually a single small median scale.

The side of the body between the large vertebral scales and the large ventral scales is covered with many small granular scales and fewer enlarged, almost tubercle-like scales disposed in roughly oblique rows. Granular scales predominate in an area adjacent to and as wide as the vertebral rows, except for a row of slightly enlarged, keeled scales that alternate with the vertebrals.

The tubercle-like scales extend from the side of the body forward onto the side of the neck and dorsally onto the nape between the enlarged post-parietal scales and the anteriormost pair of enlarged vertebrals.

The ventral scales are large and at the level of the abdominal glands are roughly disposed in tranverse rows 8 scales in breadth. Each ventral scale, except for those covering the abdominal glands, bears a small median keel and is drawn out to a point posteriorly. The scales covering the abdominal glands are smooth and lack the keel and posterior point. There are two large, keeled, preanal scales.

The scales of the limbs are rather strongly keeled, the keels being drawn up into almost tubercle-like projections on the scales of the upper and outer surfaces of the hind leg.

The scales of the tail are keeled and arranged in annuli.

The digits are covered above by single scales throughout most of their entire length, although at their base there may be 1 or 2 paired scales (Group 1 of Brongersma, 1942). There are 20-29 (17 on one apparently normally developed toe; see Table I) subdigital lamellae on the 4th (longest) toe. The lamellae on the basal third of the toe consist of paired scales, one scale being large and covering most of the subdigital surface and the other scale being small and laterally situated. The lamellae on the distal ⅔ of the toe are smooth and consist of single scales.

Adult males have both palmar and plantar pores. The palmar pores are few in number (2-4), and are distributed in an arc on the anterior edge of the palm. The plantar pores (3-10) are distributed in two rows across the sole: a longer series from the extreme base of the 4th toe and a shorter series from the base of the 3rd toe. In larger males there may be one or two pores on the base of the 5th toe.

Females always lack palmar pores, and whereas all females have large plantar scales similar to those bearing pores in males, the

pores are developed in only some females. When present in females the plantar pores are less well developed and less numerous (1-6) than in males.

There is a pair of abdominal glands which are covered by 2 pairs of midventral scales lacking keels and the posterior median point.

Color (Fig. 2): In preservative, specimens are generally brown above and on the sides and light yellowish brown below. Most individuals are uniformly dark above, but some show various degrees of light tan to whitish mottling on the nape, back, and upper surface of the base of the tail. The lighter mottled pattern tends to be bilaterally symmetrical on the nape and back and is often expressed as 1 or 2 transverse, posteriorly projecting chevrons on the dorsal base of the tail.

Variation: There is a slight difference in the dorsal color of the Bougainville and Buka specimens (Fig. 2). *Pseudoponceleti* from Bougainville tend to be darker brown dorsally with less light mottling than is found in Buka specimens. In Buka *pseudoponceleti* the light dorsal color tends to be more pronounced, with a few individuals being predominately creamy tan on the body with some brown mottling.

The general differences in color pattern between the Buka Island and Bougainville populations are correlated with differences in the distribution of certain scale counts between the two populations (Table 1). Using the coefficient of difference (C.D.) statistic (Mayr, *et al.*, 1953) to determine the degree of joint non-overlap between the Bougainville and Buka populations in regard to these differences, the C.D. was found to be lower in each case than the minimum C.D. of 1.28 and 90 per cent joint non-overlap convention commonly accepted for giving subspecific recognition to two populations. These differences do not, therefore, seem to warrant subspecific recognition for the Bougainville and Buka populations.

Distribution (Fig. 1): *Tribolonotus pseudoponceleti* has been collected at several localities on Bougainville as well as on Buka, just north of Bougainville (Fig. 1). Altitudinally, the species is known from the coastal lowlands up to an elevation of about 4000 feet (in an area 7-8 miles east of Kunua, Bougainville). None of these skinks has ever been taken by Parker or his native collectors on the Buin Plain at the south end of Bougainville, however. In this region the species was only found from about 2000 feet and above in the mountains.

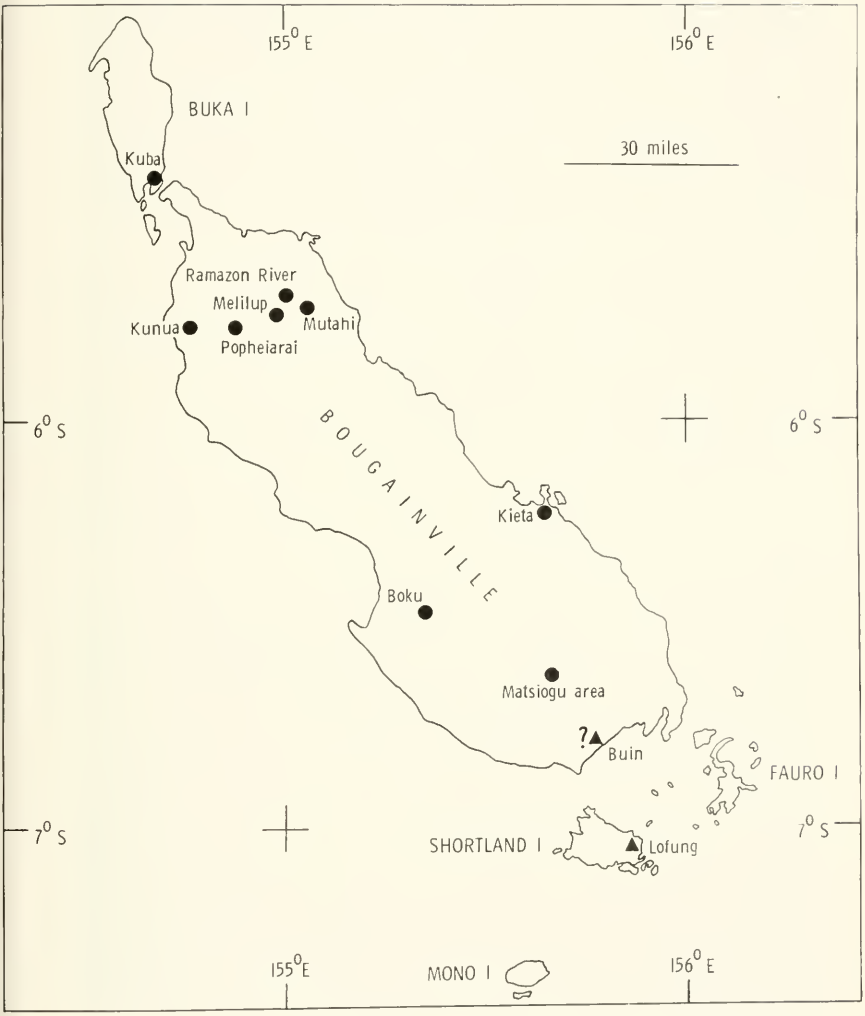

Figure 1. Map of Bougainville and surrounding islands showing the known collecting localities for *Tribolonotus psendoponceleti* (circles) and *T. ponceleti* (triangles).

It is curious that the species was not found on Shortland in the Bougainville Straits, approximately 6.1 miles south of Bougainville. This smaller island is separated from Bougainville by a sea passage not more than 25 fathoms in depth and was probably connected with the mainland during the Pleistocene.

Comparisons: As Zweifel (1966) has provided a detailed comparison between *annectens* and *pseudoponceleti* (under the name *ponceleti*) as well as between *annectens* and other species of the genus, the comparisons in this section are limited to *annectens* and *ponceleti* and are intended to complement Zweifel's recent discussion.

In his diagnosis of *annectens,* Zweifel (1966) noted that the "ventral scales number 40 in *T. annectens;* 44 to 54 (mean 48.6) in 45 specimens of *T. ponceleti.*" This particular difference between *annectens* and *pseudoponceleti* (Zweifel's *ponceleti*) is, however, less clear cut with the additional data now at hand. There are, indeed, generally more gular and ventral scales[1] in Bougainville (whence came all but one of the specimens of *pseudoponceleti* (42-54, avg. = 48.4) than in *annectens* (40 in the type, 46 in the Copenhagen specimen; avg. = 43.0), but the Buka Island population of *pseudoponceleti* has a somewhat intermediate number of gular and ventral scales (42-49, avg. = 45.0).

Until now *ponceleti* was known in the literature only from the single individual of the original description. Parker has, however, recently obtained two more specimens for the Museum of Comparative Zoology, which have allowed us to make direct comparisons between *ponceleti* and *pseudoponceleti.*

Other than size (see Diagnosis) there are several subtle differences in squamation between *pseudoponceleti* and *ponceleti.* In *pseudoponceleti* the first supralabial and infralabial, which are long and thin, extend posteriorly to at least the level of the anterior corner of eye, whereas in *ponceleti* the first supralabial and infralabial extend posteriorly only to a point about half way between the snout and the anterior corner of the eye. The position of the first supralabial thus permits the second supralabial to form a suture with the nasal in *ponceleti,* but in *pseudoponceleti* the first

[1] Counted along the ventral midline from the enlarged, paired chin scales to, but not including, the large, paired preanal scales (Zweifel's 1966 standardization). Presumably Zweifel's use of "ventral scales" in the preceding quote of this paragraph is meant to include the gular scales also.

supralabial meets the loreal, separating the second supralabial from the nasal. In *pseudoponceleti* the enlarged vertebral scales become poorly defined just anterior to the level of the insertion of the forelimbs, but in *ponceleti* the enlarged vertebral scales maintain their continuity farther on to the nape. The keels of the vertebral scales and two rows of tubercles just lateral to the vertebral scales are relatively larger and more pronounced in *ponceleti* than in *pseudoponceleti.* The one or two scales situated in the dorsal midline between a preceding and following pair of enlarged vertebrals are also relatively larger in *ponceleti* than in *pseudoponceleti.* There are two rows of plantar pores in male *pseudoponceleti,* one extending from the base of the 4th toe onto the sole and the other extending from the base of the 3rd toe onto the sole. In male *ponceleti* there is only one row of pores extending from the base of the 4th toe.

Breeding: T. pseudoponceleti is oviparous and lays but one oblong, leathery, shelled egg in a clutch. Furthermore, the left oviduct is reduced to a small, vestigial appendage of the cloaca leaving the right as the functioning oviduct. In only two of 101 females with oviducal and/or ovarian eggs collected at Kunua, Bougainville, was there a small yolky egg in the reduced left oviduct. These 2 eggs, however, did not appear to be viable.

It is noteworthy that the left ovary is still functional. Ten of the 101 females with oviducal and/or ovarian eggs had a single large yolky egg in the left ovary, but in all 10 females the left ovary had shifted to the right side, where, presumably, the ovulated eggs would pass into the right oviduct, i.e., the only functional oviduct. In no case was a large ovarian egg found in the left ovary when it was in its normal position on the left side of the body cavity. These data would indicate that as yolking proceeds in a follicle of the left ovary, the ovary is displaced to the right side, perhaps as a result of "crowding" with other internal organs, e.g., the stomach which tends to lie more on the left side of the body.

It would appear that ovulation of a second egg may occur just prior to or just after depositon of a preceding egg. This supposition is based on observations of single oviducal eggs the same size as the largest ovarian egg in the right oviduct just anterior to a full term egg in the same oviduct. In other cases there is simply a large ovarian egg and no oviducal egg. Such a situation would pertain if a full term oviducal egg had been laid just before ovulation of the second egg.

The 101 females with large ovarian eggs and/or oviducal eggs ranged in snout-vent length from 44-58 mm (avg. = 51.8 mm).

The smallest female contained a large, shelled oviducal egg. Given the large total sample size, it would appear that 44 mm is near the snout-vent length at which females first become capable of reproducing.

Ecology: T. pseudoponceleti is sympatric with *T. blanchardi* on Bougainville, although the two species occur in rather different ecological situations.

T. blanchardi is a montane species, and is probably to be found throughout the mountain ranges in the center of Bougainville. Specimens have been collected at 2000-3000 feet in the ranges north of Buin. Other specimens from the ranges east of Kunua were collected in river valleys from about 500-3000 feet. The habitat varies somewhat with altitude. In the lower altitudes where the ridges are still warm and comparatively dry, the species lives only in the steep sided and heavily shaded small creek valleys. At higher altitudes the species occurs farther from the waterways, but is still easier to collect along the creeks. The lizard does not live in the open in any environment, but prefers tall, shaded, primary forest and abundant moisture. In river and creek beds individuals are found under stones, logs and leaf rubbish at, and just above, water level, but only very occasionally may one be found moving on the ground. It often is found in company with *Sphenomorphus cranei* and *S. concinnatus.*

T. pseudoponceleti has a greater altitudinal range (coast to above 4000 feet) than *T. blanchardi,* but it is found more frequently at lower altitudes. *T. pseudoponceleti* is terrestrial and very secretive, living in and under decayed logs in all its types of habitat. It is common in swampy areas, and in some places is common on the plains where it is found in primary forest and in secondary growth. In addition, newly cleared gardens usually contain numbers of these skinks. The species likes moist conditions but not the very wet conditions preferred by *blanchardi.*

In the mountains there is little syntopy between the two species, because while *blanchardi* is confined to creek beds initially, then the shaded slopes of the steep ridges, *pseudoponceleti* is to be found only on the sharp ridges where the scrub is more open and the ground drier and warmer. This restriction to the ridges has been confirmed by extensive collecting east of Kunua from 2000-4000 feet. A number of other coastal species which range to about 2000 feet in the mountains are also confined to the drier ridge tops.

In the Boku area the natives believe *pseudoponceleti* prefers the hairy base of a large ground fern as a dwelling place, but this was not borne out by the breaking up of a number of these ferns in a

hunt for the species. The habitat in this area was decaying wood on the ground.

Whether *T. ponceleti* also occurs on Bougainville along with *pseudoponceleti* and *blanchardi* is uncertain. The single specimen from which the species was described (Kinghorn, 1937) was said to have come from "Buin, east Bougainville Island, Solomon Islands." However, there are no *ponceleti* among several hundred reptiles that Parker and his native collectors obtained in southern Bougainville near Buin.

Upon inquiry, Mr. Harold Cogger of the Australian Museum found the notes that accompanied Father J. B. Poncelet's zoological collection of which the single specimen of *ponceleti* was a part. The notes consist mainly of a list of the common English and native names for each of the specimens and are prefaced by an unequivocal statement regarding the provenance of the collection — "All those (*sic*) specimens have been collected at Buin (South Bougainville), 10 to 15 miles in the interior, during the months of September and October 1934, by Father J. B. Poncelet S.M., of the Buin Catholic Mission."

Native collectors have obtained the only other two known *ponceleti* at Lofung on Shortland Island (Fig. 1), but whether this large *Tribolonotus* also occurs on Bougainville is still an open question.

The presence of *ponceleti* and the absence of *pseudoponceleti* on Shortland Island seems well established. It is also fairly clear that *pseudoponceleti* is absent from the Buin Plain. It is not certain whether *ponceleti* occurs on the Buin plain, although it is fairly well established that *ponceleti* does not occur elsewhere on Bougainville where large collections have been made (Fig. 1). Reasons for the absence of *pseudoponceleti* from the Buin plain and Shortland Island are obscure as are the reasons for the absence of *ponceleti* from the rest of Bougainville, if this species occurs on Bougainville at all. There seem to be few ecological differences between the Buin plain, the other lowland areas of Bougainville where *pseudoponceleti* has been collected, and Shortland Island (Parker, personal observation).

As no noticeable ecological differences are known to be correlated with the ranges of *ponceleti* and *pseudoponceleti*, the only likely remaining explanation for their allopatry is possibly competitive exclusion — perhaps of a very dynamic nature. But this facile explanation seems implausible, as the great size difference between the two species would certainly suggest a difference in the utilization of the habitat by the two species.

On the basis of our present information there is little more that can be said beyond this description of the problem. The ecologic and geographic relationships of *ponceleti* and *pseudoponceleti* will be interesting field problems for future workers on Bougainville.

Little seems to have been published on the ecology or habits of the closely related species *T. gracilis* and *T. novaeguineae*, but Mr. Harold Cogger has written to us about his personal experience with *T. gracilis*. Mr. Cogger says, "I am familiar with this species only on Karkar Island, where I obtained approximately 90 specimens. All specimens collected by me, or in my presence, were found under decaying logs and other vegetation usually on the banks of small non perennial streams, up to an altitude of about 2,000 feet, usually in fairly dense primary or secondary forest."

Behavior: T. pseudoponceleti is cryptic in its habits and never moves about in the open. No lizards were ever collected or seen in the open, and none was found moving about at night. In captivity they will come into the open parts of the cage to eat if there is little or no light. When found in its usual habitat under logs *pseudoponceleti* makes no attempt to escape but may move away slowly if given time. When an individual is uncovered there seems to be an instinctive reaction to flatten on the ground to avoid being noticed.

Usually two adults, a male and a female, are found together, and occasionally, if the log is large enough, another pair or two or three partly grown specimens may be close by. Rarely is a lone individual found — a close search into the ground and log nearby usually reveals a second individual.

T. pseudoponceleti is not strictly speaking a burrower but moves through insect burrows and hollows in and under logs. In captivity the species will eat termites. The lizards seem to be keen sighted and can detect movements in a dimly lit room some 10-15 feet away from the cage containing captive skinks. Other species of skinks of different genera seemed to be able to detect similar movements only when within 5-6 feet of the cage.

T. blanchardi is very similar to *pseudoponceleti* in its behavior. It moves slowly, although when being chased it will make short bursts of speed to escape. In captivity it is not given to the quick, nervous movements found in other skinks, e.g., *Emoia* and *Sphenomorphus* species, either when frightened or feeding. When moving, the skink holds the whole body and sometimes the tail off the ground.

Virtually nothing is known of the ecology or habits of *ponceleti*. The two specimens of *ponceleti* collected for Parker by the natives at Lofung, Shortland, had dirt in the crevices between the scales

which may indicate that the species is something of a burrower. Many *pseudoponceleti* also have dirt between their scales when collected and this species is known to spend much of its time in close contact with the soil in secretive situations.

VOLAR PORES AND ABDOMINAL GLANDS IN THE GENUS *TRIBOLONOTUS*

Among lizards, volar pores and the dermal abdominal glands are unique to the genus *Tribolonotus*. The presence of volar pores was first pointed out by Roux (1930) in male *T. schmidti* when he used them as a character diagnostic of a new genus — *Pediporus*. Roux (1934) later rectified this mistake when he found similar pores on some of the toes and sole of a male *T. novaeguineae* — the type species of the genus *Tribolonotus*.

Parker (1940) extended Roux's observations on volar pores of *gracilis* and provided additional information on their distribution in *schmidti* and *novaeguineae*. Parker also provided the first account of abdominal glands in the genus, having noticed them in male *gracilis* and *novaeguineae*.

Function: The function of both volar pores and abdominal glands is speculative. Secretion seems to be the primary purpose of both structures, and from the distribution of the glands on the body of the animal — belly and volar surfaces — it would seem as though the secretion would be placed in a new part of the microenvironment with every step taken by an animal. What, then, is the value of such a secretion?

The only information we have on the ecology of *Tribolonotus* is that given above for *blanchardi*, *pseudoponceleti*, and *gracilis*. All three species appear to be highly secretive and spend most of their time under objects such as stones, leaf rubbish, and rotten logs — microhabitats that are both dark and relatively moist, and if the secretions are volatile and odiferous, they might be important olfactory signals.

Furthermore, the fact that both structures are generally better developed in adults than juveniles and in males rather than females suggests that their function may have some sexual significance. For instance, the secretions provided by the pores and glands may be olfactory markers of territory.

Distribution of volar pores in Tribolonotus (Table 2): The two known specimens of *annectens* are females and both lack volar pores.

Plantar pores occur in both male and female *pseudoponceleti* where they are found in a series behind both the 3rd and 4th toe. In some males, but never in females, there may be an additional pore or two on the basal third of the 5th toe. Palmar pores are present in males but not in females.

The three known specimens of *ponceleti* are males and all have a single series of plantar pores directly in line with the 4th toe (Fig. 3). Palmar pores are absent.

Both *gracilis* and *novaeguineae* females apparently lack volar pores. Males of both species have pores on the basal half of the 3rd and 4th toes and on the sole in a line directly behind the 3rd toe. Male *gracilis* possess palmar pores (personal communication, Harold Cogger *re* Karkar Island *gracilis*), but whether palmar pores are present or absent in male *novaeguineae* is unclear as yet.

Female *blanchardi* also lack volar pores. Males have both palmar and plantar pores which are distributed mainly on the palm and sole, although occasionally a pore is found on the basal third of one of the digits.

In *schmidti,* females lack volar pores, but males have both palmar and plantar pores, the latter being distributed in two series: one behind the 4th toe and a second, shorter, series behind the 3rd toe.

Distribution of abdominal glands in Tribolonotus (Table 2): In the Copenhagen specimen of the female *annectens* which we have examined, the glands are covered by four pairs of median ventral scales.

Both sexes of *pseudoponceleti* have a single pair of unlobed abdominal glands lying beneath two pairs of midventral scales. The glands are slightly smaller in females than in males.

In *ponceleti,* which is at present known from only 3 males, the abdominal glands are bilobed and covered by one or two pairs of ventral scales (Fig. 3).

Female *gracilis* and *novaeguineae* lack abdominal glands, but in males of both species the glands are paired and unlobed and extend a distance of three or sometimes four ventral scales along the midline.

Female *blanchardi* also lack abdominal glands. Males have four pairs of bilobed abdominal glands which extend the length of four or five ventral scales.

The glands are very small and minutely lobed in female *schmidti,* but the ventral scales covering the glands are not visibly different from the other ventral scales. In males the two pairs of ventral scales covering the glands are characteristically smooth along their posterior edges rather than mucronate as are the surrounding enlarged ventral scales.

REPRODUCTION IN *TRIBOLONOTUS*

The mode of reproduction is known for all the species of *Tribolonotus* except *ponceleti* which is known from only 3 male specimens. From an examination of gravid *annectens* (also see Zweifel, 1966:2), *blanchardi, gracilis* and *novaeguineae,* as well as *pseudoponceleti,* it would appear that these species are oviparous and produce but a single oblong leather shelled egg in a clutch in which little or no embryonic development takes place prior to deposition.

Schmidti is atypical of the genus in producing living young but typical in producing but one young at a time. Roux (1930:133) says of a single female he received from Guadalcanal, Solomon Islands, "Elle renferme un embryon bien developpe." The adaptive significance of live-bearing habits in *schmidti* are difficult to imagine and will probably remain obscure until more is known of the species' behavior and ecology.

It is interesting to note that *blanchardi* and *schmidti* are similar to *pseudoponceleti* in having only one functional oviduct, the right. In *blanchardi* and *schmidti* as in *pseudoponceleti* the left oviduct is reduced to a small vestigial appendage of the cloaca. In *blanchardi* the left ovary is still functional, and, as in *pseudoponceleti,* is usually displaced to the right side prior to ovulation. In *schmidti,* on the other hand, the left ovary is either absent or greatly reduced in size; in the latter case it is situated well posteriorly in the body cavity and is probably not functional.

Unfortunately the state of preservation of the four gravid *gracilis* and single gravid *novaeguineae* available for study was such that the condition of the left ovary and oviduct could not be interpreted.

These data are of further interest on two counts. First, it may well be that a single egg or young is characteristic of the taxon *Tribolonotus.* Such specificity in the number of eggs produced is not unusual in some groups, e.g. geckos, but it is unreported in any supraspecific taxa of skinks.[1]

Second, a single functional oviduct has been previously unknown in reptiles except in some leptotyphlopids and typhlopids (Guibé, 1948; Robb, 1960; Fox and Dessauer, 1962). In these "worm snakes," as in *Tribolonotus,* it is the left oviduct that is non-functional. The left ovary in the leptotyphlopids and typhlopids is slightly smaller in size than the right ovary, although it is still

[1] Many *Emoia,* however, especially the smaller species, have but two eggs in a clutch (Greer, 1968).

functional. The left ovary seems to have lost all function in *Tribolonotus schmidti*, but the large ova discovered in the left ovary of a few individuals of both *blanchardi* and *pseudoponceleti* would indicate that this organ is in some cases still functional in these species.

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Dr. E. E. Williams of the Museum of Comparative Zoology has also read the manuscript in several versions and has smoothed over many "rough spots" with each reading.

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TABLE 1

Frequency distribution for several meristic characters in the two island populations of *Tribolnotus pseudoponceleti*

BOUGAINVILLE

Enlarged, paired middorsal scales

x	21	22	23	24	25	26	$N = 114$
							$\bar{x} = 23.8$
f(x)	1	3	32	64	13	1	$\sigma = 0.75$

Gular + ventral scales

x	45	46	47	48	49	50	51	52	53	54	$N = 106$
											$\bar{x} = 48.4$
f(x)	8	8	17	26	22	10	9	1	3	2	$\sigma = 1.97$

Subdigital lamellae 4th toe

x	17	20	21	22	23	24	25	26	27	28	29	$N = 211$
												$\bar{x} = 23.9$
f(x)	1	2	18	24	44	41	44	18	15	3	1	$\sigma = 1.83$

BUKA ISLAND

Enlarged, paired and middorsal scales

x	22	23	24	25	$N = 22$
					$\bar{x} = 23.8$
f(x)	1	6	12	3	$\sigma = 0.77$

Gular + ventral scales

x	42	43	44	45	46	47	48	49	$N = 22$
									$\bar{x} = 45.0$
f(x)	1	6	3	3	3	4	1	1	$\sigma = 1.95$

Subdigital lamellae 4th toe

x	20	21	22	23	24	25	$N = 42$
						$\bar{x} = 21.8$
f(x)	3	14	15	8	1	1	$\sigma = 1.06$

TABLE 2

Distribution of volar pores and abdominal glands in the sexes of the seven known species of *Tribolonotus*

	Palmar pores		Plantar Pores		Abdominal glands	
	♂	♀	♂	♀	♂	♀
annectens	?	—	?	—	?	+
pseudoponceleti	+	—	+	+	+	+
ponceleti	—	?	+	?	+	?
gracilis	+	—	+	—	+	—
novaeguineae	?	—	+	—	?	—
blanchardi	+	—	+	—	+	—
schmidti	+	—	+	—	+	+

TABLE 3

Species, number of specimens, snout-vent length, number of eggs/female, and comments on reproductive state of gravid *Tribolonotus* examined

Species	Number of gravid ♀♀ examined	Snout-vent length (mm)	Number of eggs/♀	Comments
annectens	2	49-50	1	"One large egg evidently nearly fully developed" in the type (Zweifel, 1966). Second egg in Copenhagen specimen with thick shell.
pseudoponceleti	101	44-58	1	Yolky ovarian eggs to large, leathery-shelled oviducal eggs.
gracilis	4	87-100	1	1 yolky ovarian egg; 3 large, leathery-shelled oviducal eggs.
novaeguineae	1	75	1	1 leathery-shelled oviducal egg.
blanchardi	9	31-36	1	Yolky ovarian eggs to large, leathery-shelled oviducal eggs.
schmidti	12	34-38	1	Yolky ovarian eggs to terminal young.

Figure 2. Paratypes of *Tribolonotus pseudoponceleti* from Bougainville (MCZ 72914) and Buka (MCZ 67713), exemplifying the differences in dorsal coloration between the two island populations.

72914
67713

Figure 3. *Tribolonotus ponceleti* from Lofung, Shortland Island. Notice the pair of ventral scales overlying the abdominal glands, and the plantar pores in the ventral view of the specimen.

9244

BREVIORA

Museum of Comparative Zoology

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HERPETOGEOGRAPHY OF PUERTO RICO. V. DESCRIPTION OF A NEW SPECIES OF *SPHAERODACTYLUS* FROM DESECHEO ISLAND

Harold Heatwole[1]

INTRODUCTION

The Puerto Rican island shelf (Greater Puerto Rico) has received considerable attention from herpetologists, and the herpetofauna of the larger islands is now reasonably well known. However, the small islands and keys, with some exceptions, have not been studied in a thorough way. A faunal survey of these islands is now in progress (Levins and Heatwole, 1963), and some of the results have been published (Heatwole *et al.*, 1963, 1965; Rolle *et al.*, 1964; Heatwole and Torres, 1967). The present paper represents a further contribution in that direction.

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DESECHEO ISLAND

Desecheo is a hot, dry, relatively steep-sided island located in the Mona Channel 12 miles west of Punta Higüero, P. R. It consists largely of volcanic rock, although some limestone deposits are present. It has a diameter of 1 mile and a maximum elevation of 715 ft. (U. S. Dept. Comm. Coast and Geodetic Survey, 1962). The vegetation is cactus scrub and xeric woodland. Large numbers of

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Boobies nest on the island; terrestrial hermit crabs form a conspicuous faunal element. Though uninhabited by humans, a small herd of feral goats is present.

Its known herpetofauna consists of 4 species: *Alsophis portoricensis* (Grant, 1932), *Ameiva desechensis* (Heatwole and Torres, 1967), an *Anolis* reported by Wetmore (1918) to be intermediate between *A. cristatellus* and *A. monensis* (now being studied by the author), and the new species of *Sphaerodactylus* described below.

No specimens of *Sphaerodactylus* from Desecheo were available to Thomas and Schwartz (1966), and they singled out this island as "one of the few West Indian islands from which *Sphaerodactylus* has not been reported." The present study fills in this gap. All scale counts were made after the method of King (1962).

Sphaerodactylus levinsi sp. nov.[1]

Holotype: UPRRP 4566 (donated to the Museum of Comparative Zoology, Harvard University, MCZ No. 100274), a male taken 28 May 1965 on Desecheo Island, Puerto Rico, by the author.

Paratypes: UPRRP 4565, 4567, 4570 (males), and UPRRP 4571-72 (females), collected 27-29 May 1965 on Desecheo Island, P. R., by the author, R. Levins, and F. MacKenzie.

Distribution: Known only from the type locality, Desecheo Island, where it is not abundant; found chiefly under stones and dead wood at the edges of dry drainage gullies.

Diagnosis: A species of *Sphaerodactylus* characterized by: (1) a prominent light-colored frontal bar, bordered by brown completely separating it from other light-colored areas (Fig. 1), (2) shoulder patch not bordered by a lighter color but enclosing two white, round ocelli, (3) lack of sexual dichromism, (4) scale rows around mid-body 46-48, and (5) lamellae under 4th toe 7-8.

Description of holotype: An adult male with snout-vent length of 28.2 mm; dorsal scales axilla to groin 28, ventral scales axilla to groin 31; mid-body rows of scales 48; 4th toe lamellae 8; internasals 1; supralabials to mid-eye 3; escutcheon 5 by 17 scales; dorsal scales keeled, imbricate, no microscopic hairs or knobs detected; no granular dorsal scales; ventral scales smooth, nearly round.

[1] This species is named in honor of Dr. Richard Levins, who was a stimulating and pleasant companion on expeditions to more than 100 islands and keys of the Puerto Rican shelf, and who contributed to this and other studies by collecting many herpetological specimens. The abbreviation UPRRP refers to the collections of the University of Puerto Rico (Rio Piedras).

venter dirty white; dorsal ground-color brown with darker brown spots tending to be aligned in longitudinal rows; a U-shaped, dark brown mark over sacrum; head pattern with a dark brown medial preorbital stripe diverging anterior to the eyes to enclose a longitudinal, conspicuous, light-colored bar (frontal bar), extending nearly to the occipital region, where the brown stripes re-converge, isolating bar from other light-colored areas; lateral, dark brown preorbital stripes diverge around eye and extend separately across the temporal region to break up into spots near the shoulder; prominent, round dark brown occipital spot followed posteriorly by two pairs of faint spots; no well-defined nuchal spot; oval, dark brown shoulder patch enclosing a pair of light-colored ocelli. Ocelli and frontal bar are near-white and are conspicously lighter than any other features; occipital spot and shoulder patch (near-black) conspicuously darker than any other feature.

Variation: Coloration was extremely uniform, and the description of the holotype could serve almost equally well for any of the other specimens examined, including both sexes, except for (1) varying tendencies of the lateral head-stripes to coalesce with the faint spots behind the occipital spot, and (2) a narrow line running anteriorly from the occipital spot to connect with the brown color enclosing the frontal bar in two specimens (males). Escutcheons were 4-6 by 12-17 in scale number; 4th toe lamellae were 7 or 8; upper labials were 3 or 4; internasals did not vary (always 1); scale rows around mid-body were 48 with one exception (46); dorsal rows axilla to groin varied from 27 to 32 (mean 29.0; standard error 0.82) and ventral ones axilla to groin from 28 to 32 (mean 29.8; standard error 0.66).

Relationships: S. levinsi is most closely related to *S. monensis* and *S. macrolepis*. It is distinguished from *S. macrolepis* by its higher number of dorsal scales, its lower number of toe lamellae, and by lacking sexual dichromism. It differs from *S. monensis* by lacking a light border around the scapular patch and by having round rather than transverse ocelli. The conspicuous frontal bar (Fig. 1) is not shared with either species.

Thomas and Schwartz (1966) have suggested that with the possible exception of *S. beattyi* of St. Croix all the *Sphaerodactylus* on the Puerto Rican shelf are the result of radiation from a single ancestral invading stock. According to their scheme, a proto-*macrolepis* form separately gave rise to *S. roosevelti* and *S. monensis*, before continuing on to modern *macrolepis*, which in turn gave rise to two other species groups as well as a variety of subspecies.

S. monensis is now found only on Mona Island (about 40 miles west of Puerto Rico), and *S. levinsi* only on Desecheo Island (12 miles west of Puerto Rico). I suggest that the proto-*macrolepis* ancestor succeeded in reaching Mona and Desecheo, where it separately gave rise to the two present-day forms. Heatwole and MacKenzie (1967) have shown that during the Pleistocene, conditions were much more favorable for flotsam transport from Puerto Rico to both Mona and Desecheo than they are now. The southwestern coast of Puerto Rico extended considerably farther into the Mona Channel, thereby reducing inter-island distances and also deflecting currents in more favorable directions. At maximum extension, the current passing westward along the southern coast of Puerto Rico would have proceeded almost directly toward Mona, and it was probably at this time that proto-*macrolepis* arrived there. As the southwestern coast of Puerto Rico subsequently receded, it would have permitted the current to swing increasingly toward its present northward direction through the Mona Channel. Then Desecheo, rather than Mona, would have been in the more direct path of the current. Land configuration was also conducive to eddy currents between Desecheo and Punta Higüero, Puerto Rico. On the one hand, this probably caused increased isolation of the Mona population, permitting its differentiation into *S. monensis,* and on the other, made possible flotsam transport of proto-*macrolepis* to Desecheo. Gene flow via flotsam transport of animals was probably maximal between Puerto Rico and Desecheo at that time, as further recession of the southwestern coast increased the effective inter-island distance and resulted in currents less favorable for flotsam transport between them. Today, any flotsam reaching Desecheo would have its most likely origin on the extreme southwestern tip of Puerto Rico, rather than geographically nearer points. This increased isolation undoubtedly facilitated divergence of the Desecheo population to form *S. levinsi.*

Additional evidence for the isolation of the Mona population before that of Desecheo is that the former has retained a light border around the scapular patch, a character no longer present in the western populations of *S. macrolepis* or in *S. levinsi.*

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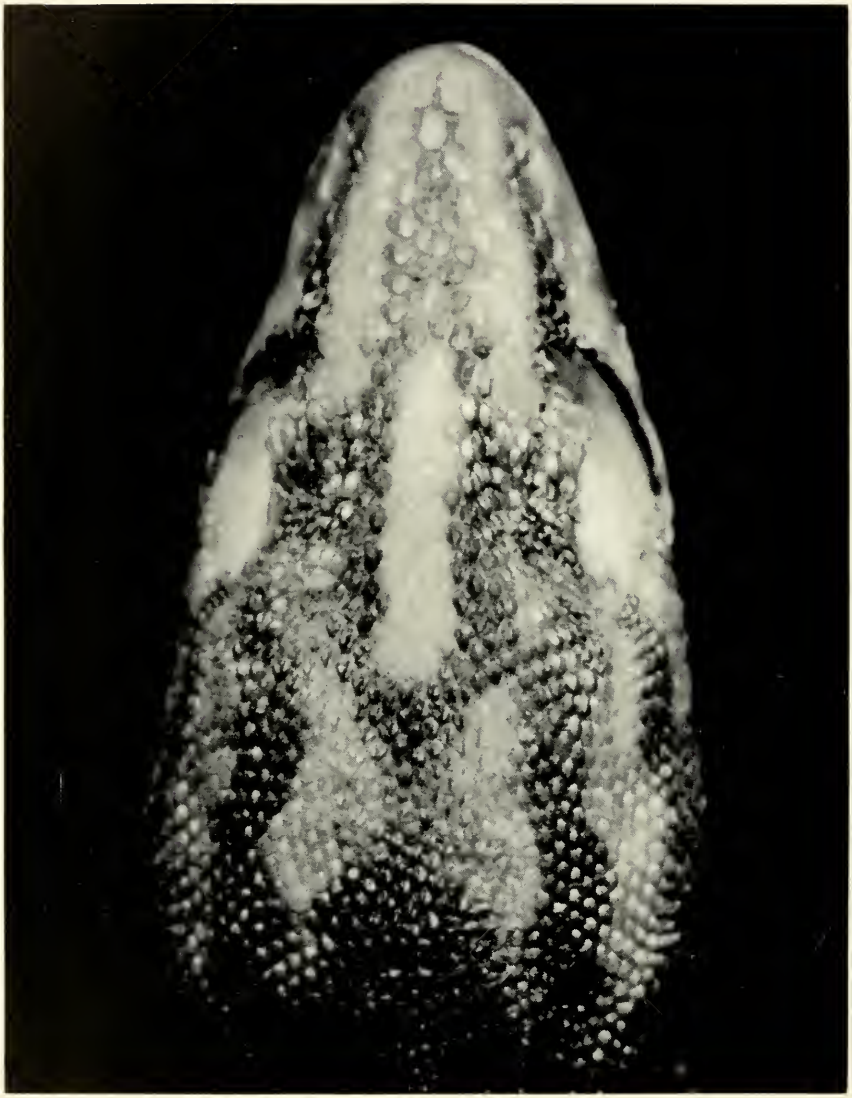

Figure 1. Head of holotype of *Sphaerodactylus levinsi*.

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Museum of Comparative Zoology

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INTRA- AND INTERSPECIFIC CHROMOSOME VARIATION IN THE LIZARD *ANOLIS CRISTATELLUS* AND ITS CLOSEST RELATIVES

George C. Gorman,[1] Richard Thomas,[2] and Leonard Atkins[3]

INTRODUCTION

Widespread on the Puerto Rican bank (Puerto Rico, its offshore keys, and the Virgin Islands, excluding St. Croix) is the common lizard *Anolis cristatellus*. Data on its ecological distribution have been summarized by Rand (1964). The last taxonomic revision (Grant, 1931) recognized three subspecies: *A. c. cristatellus*, found virtually throughout Puerto Rico, *A. c. wileyae*[4] from the islands east of Puerto Rico, including both the adjacent keys and the Virgin Islands, and *A. c. cooki* from the extremely dry, desert-like southwestern part of Puerto Rico. Thomas (1966) used the combination "*Anolis cooki*" in a discussion of the endemicity of the herpetofauna of southwestern Puerto Rico but did not justify his usage. *Anolis monensis* on the island of Mona to the west of Puerto Rico has been considered a separate species, but it is very close to *cristatellus* and its taxonomic status needs reassessment. Unfortunately, specimens of this species were unobtainable for chromosomal analysis.

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[4] Although described by Grant as *Anolis cristatellus wileyi*, the name must be changed to take the feminine ending, as the subspecies was named after Grace Olive Wiley (Grant, 1931). (See articles 31 and 32, International code of Zoological Nomenclature.)

Evidence that *cooki* is a separate species was obtained by Albert Schwartz and David Leber in 1961 when they collected two kinds of *cristatellus*-like anoles on the islet of Caja de Muertos off the south coast of Puerto Rico. Later, Thomas observed that where *cooki* is sympatric with *cristatellus*, along coastal areas of southwest Puerto Rico, it appears to split the structural niche (terminology from Rand, 1964) by perching lower than *cristatellus*, often on rocks or on the ground rather than in trees. Although morphologically very similar to *cristatellus*, *cooki* has larger dorsal scales (Fig. 1). It also has lower 4th toe lamellar counts and keeled ventral scales, and in coloration it is typically paler than *cristatellus* and has a redder dewlap. The morphological differences are most valid when contrasted with sympatric *cristatellus*. For these reasons and for reasons presented below, we consider *cooki* a separate species. Independently, E. E. Williams has come to similar conclusions by

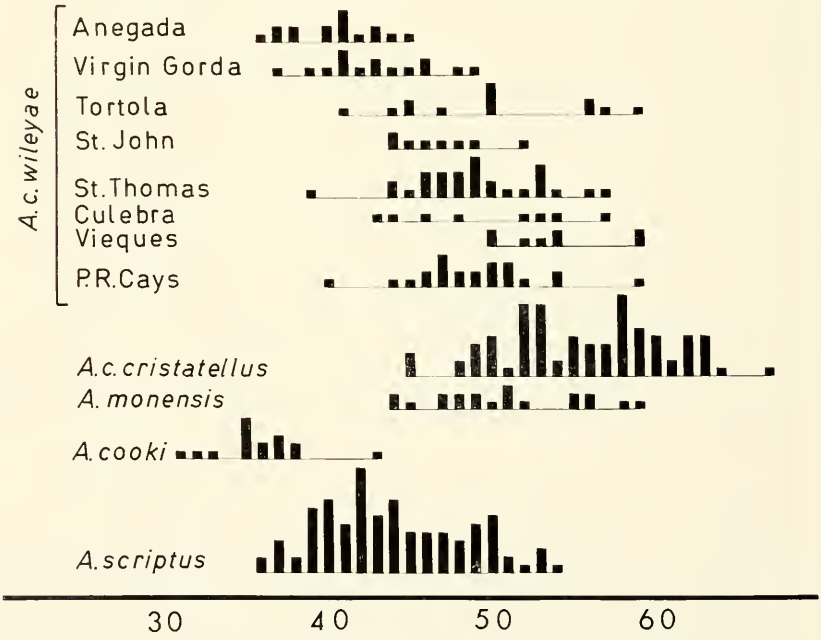

Figure 1. Dorsal scale counts (taken dorsolaterally in the standard distance) for *Anolis cristatellus* and its closest relatives. The samples for Tortola and St. Thomas include specimens from satellite islets; specimens examined are in the Albert Schwartz Field Series and the Museum of Comparative Zoology. The smallest vertical units represent single individuals.

comparison of paratypes of *cooki* with *cristatellus* from nearby localities.

The final species to be considered is *A. scriptus*, from the southern Bahamas. This species had been synonymized with *cristatellus* by Barbour (1914), but Rand (1962) showed that there were minor scale differences. He considered *scriptus* a valid species although close to *cristatellus*. Of the four described subspecies, all were recognized by Rand, and two were available for chromosomal analysis.

The forms discussed here are distinguishable by differences in coloration, especially dewlap color; their external morphology, although not always diagnostic, shows interesting regional variation. The variation in dorsal scale counts of *cristatellus* (Fig. 1) may be taken as a paradigm of trends shown by other morphological characters in this species. Tail crest height, degree of ventral scale keeling, and counts of 4th toe lamellae and loreal scales show the same pattern of variation, although the trends are generally less pronounced than are those shown by the dorsal scale counts. *A. cooki* and *A. monensis* also follow this trend in having low loreal and lamellar counts *(cooki* is extreme in its low number of lamellae). It is of interest that the *cooki* and eastern populations of *wileyae* agree with one another in having large dorsal scales, few 4th toe lamellae, few loreals, and relatively pronounced ventral keeling. This may be part of a similar adaptive constellation of characters; it should be noted that all of the small island forms *(sensu lato:* including *cooki)* show tendencies towards enlarged dorsal scales in comparison with nominate *cristatellus*.

All of these lizards belong to the *cristatellus* series, following the classification of *Anolis* into species series by Etheridge (1960). Also included in this series are four other Puerto Rican species: *krugi, pulchellus, poncensis* (grass anoles), and *gundlachi*, a species which resembles *cristatellus* and appears to replace it ecologically at high altitudes (Rand, 1964); and three species of Hispaniolan anoles, *cybotes, whitemani*, and *shrevei*, which appear very closely related *inter se* and seem to resemble most closely *A. cristatellus*.

Considerable data have already been presented on the chromosomes of *Anolis*. A karyotype consisting of six pairs of metacentric macrochromosomes and twelve pairs of microchromosomes (2n=36) is found in numerous species of *Anolis* and other iguanid lizards. This formula is considered primitive for the family Iguanidae (Gorman, Atkins, and Holzinger, 1967). Lizards with this karyotype lack obvious sex chromosomal heteromorphism, as illustrated by *A. cybotes*, a Hispaniolan member of the *cristatellus*

series (Gorman and Atkins, 1966, fig. 1 d-f). Other anoles are characterized by a reduced diploid number, and a complex sex chromosome system in which males are X_1X_2Y and females $X_1X_1X_2X_2$ (Gorman and Atkins, 1966). The karyotypes of the four Puerto Rican *cristatellus* group anoles that have already been reported on *(pulchellus, poncensis, krugi,* and *gundlachi)* are of this sort. The karyotypic difference between the Puerto Rican and Hispaniolan members of the *cristatellus* series and its phylogenetic implications are discussed elsewhere (Gorman and Atkins, in press) and will not be repeated here.

MATERIALS AND METHODS

Chromosome spreads were obtained by direct preparation of gonads or by whole blood tissue culture using a modification of the technique of Moorhead, *et al.* (1960). Techniques were outlined in Gorman and Atkins (1966). Chromosome data were obtained from 19 *A. c. cristatellus* from Puerto Rico, 14 *A. c. wileyae* from the islands east of Puerto Rico, 6 *A. cooki* from southwestern Puerto Rico, 3 *A. scriptus leucophaeus* from Great Inagua, and one *A. scriptus mariguanae* from Mayaguana. Figures 2-4 show the localities sampled in this study. For comparative purposes, data are presented on two additional Puerto Rican members of the *cristatellus* series.

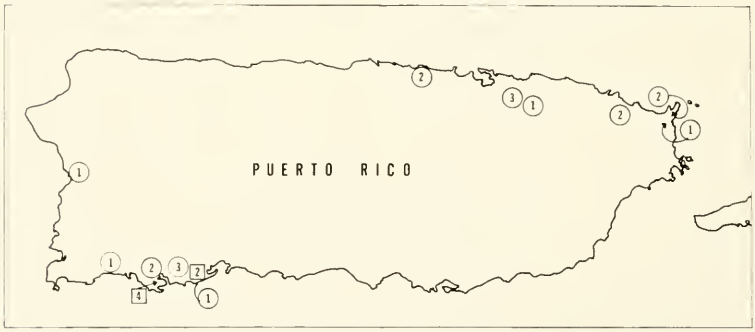

Figure 2. Localities on Puerto Rico sampled for *A. c. cristatellus* (circles) and *A. cooki* (squares). The number within each symbol is the number of specimens sampled for that locality.

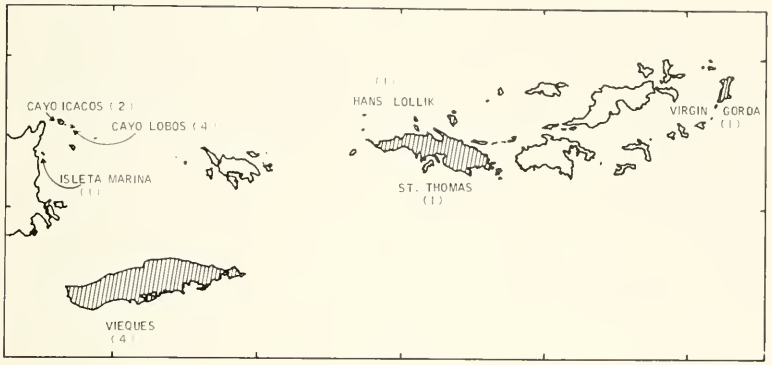

Figure 3. Map of the eastern portion of the Puerto Rico bank; islands where specimens were sampled are named. Number in parentheses is the number of specimens from each locality.

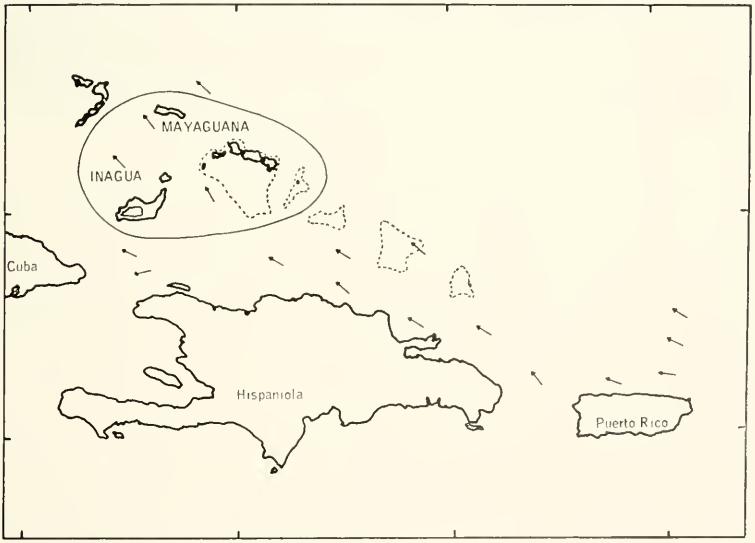

Figure 4. Map of the southern Bahamas and eastern Greater Antilles. The area enclosed in solid black represents the distribution of *A. scriptus*. Inagua and Mayaguana are the localities sampled. Dotted areas represent submerged island banks. Arrows show general trend of the currents.

RESULTS

Male meiosis. The four species in the *cristatellus* group previously studied *(gundlachi, pulchellus, poncensis, krugi,* see Gorman and Atkins, in press) are all very similar to one another. In diakinesis there are six large bivalents, two intermediate-sized bivalents, five small bivalents (13 autosomal bivalents in all), and a sex trivalent. Figure 5a shows this in *A. gundlachi.* Among the forms reported on here, only *A. cooki* has 13 autosomal bivalents and a sex trivalent. *A. cooki* differs from *gundlachi* and *pulchellus* only in the detail that the smallest bivalents do not break sharply in size when compared with the intermediates (see Figure 5b).

All *A. c. cristatellus* and both the *scriptus* subspecies differ from *cooki* and the other members of the *cristatellus* series by having one fewer autosomal bivalent. Again there are six macrobivalents; however, there are only six smaller ones, which apparently can be divided into two classes of three intermediate-sized and three small, but certainly with gradation (Figs. 5c, d).

It is among the offshore populations of *A. cristatellus wileyae* that we have made the most unusual finding. Twelve of the animals sampled appeared identical to the Puerto Rican *cristatellus* and Bahaman *scriptus,* but two others differ in having a moderate-sized body that might be a univalent. One of these animals is from the small key Cayo Lobos, the second is from Vieques. Three of the four males sampled from each of the two islands had normal meiosis (Fig. 6).

Mitosis. The mitotic metaphase of males of *cooki* is characterized by 29 chromosomes. There are six pairs of metacentric macrochromosomes and 17 smaller elements. Resolution of these elements is difficult, but there appear to be three pairs of small metacentric chromosomes, four dot-like pairs (presumably acrocentric), and three unpaired chromosomes, the largest of which is clearly metacentric and is presumably the Y (Fig. 7b). Females have 30 chromosomes and lack the unpaired metacentric. The male karyotype is similar to *pulchellus* (Fig. 7a), but again, as in meiosis, the break between size classes of chromosomes is greater in *pulchellus.* There are six pairs of metacentric macrochromosomes, two intermediate pairs of metacentric chromosomes, five pairs of microchromosomes, and, in the male, three unpaired chromosomes (2n=29).

A. scriptus and *A. c. cristatellus* have male diploid numbers of 27; female *scriptus* have 2n=28 (female *cristatellus* were not studied). The male diploid number of 27 is also found in *A. c. wileyae* (one exception will be discussed below).

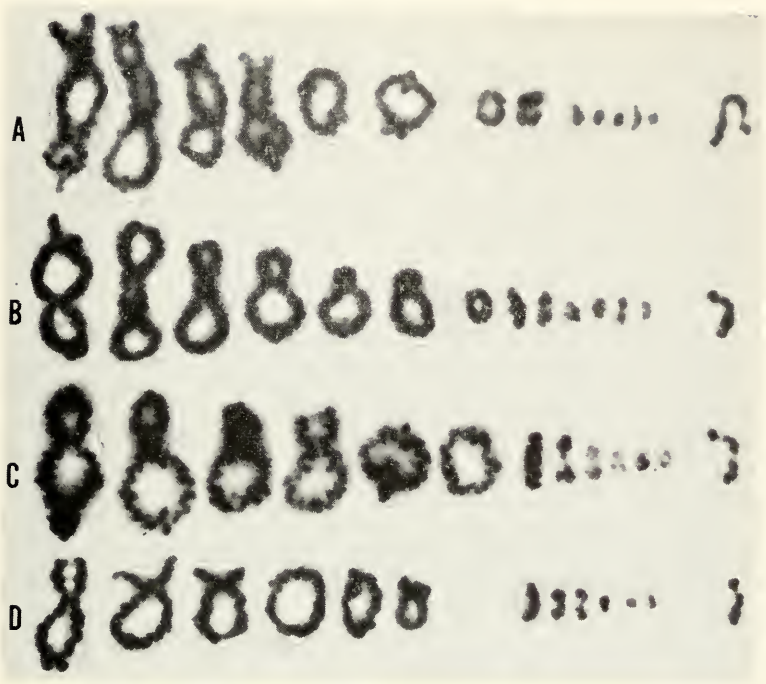

Figure 5. Meiosis in *cristatellus* group anoles. Giemsa stain.

A. *A. gundlachi.* There are six large bivalents, two of intermediate size, and five distinctly smaller bivalents; a sex trivalent is on the far right.

B. *A. cooki.* There are six large bivalents, seven ranging from intermediate to small size with no sharp break between them; and a sex trivalent.

C. *A. c. cristatellus.* There are six large bivalents, and only six ranging from intermediate to small size with no sharp break between them; and a sex trivalent.

D. *A. scriptus leucophaeus.* Quite similar to *cristatellus* directly above.

In details of karyotype, *cristatellus* and *scriptus* are very similar. There are six pairs of metacentric macrochromosomes and six autosomal pairs of small chromosomes, of which the largest three pairs are also metacentric. Males have three unpaired sex chromosomes (Figs. 7c, d).

The one exceptional animal was the *A. c. wileyae* from Vieques which had the extra body (presumed univalent) in meiosis (no mitotic divisions were seen in the specimen from Cayo Lobos that

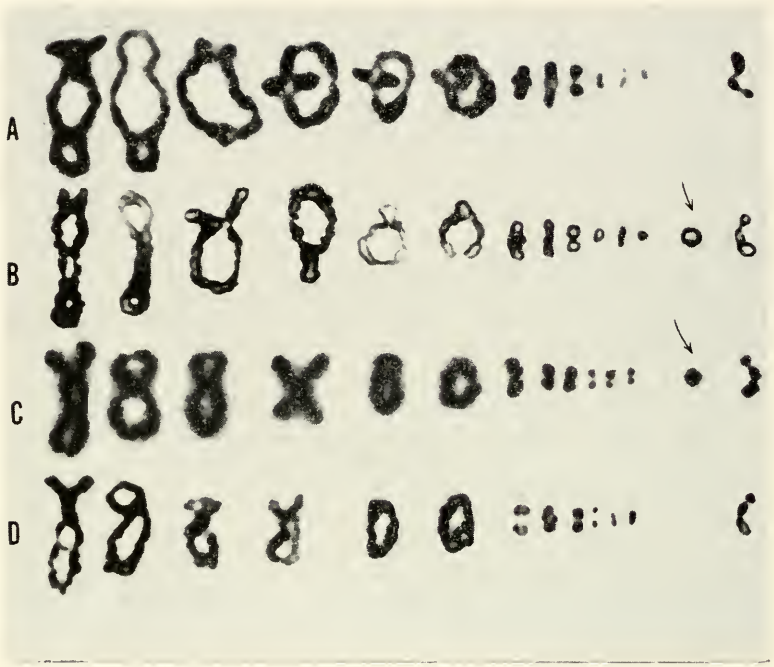

Figure 6. Meiosis in *A. cristatellus wileyae*. Giemsa stain.

A and B. Two different males from the island of Vieques. Male A is identical to typical *cristatellus*, male B has a dark staining supernumerary body (arrow).

C. A male from Cayo Lobos that also shows a dark staining supernumerary body (arrow).

D. A male from St. Thomas, Virgin Islands, which has the typical *cristatellus* complement.

had the same meiosis). Only 10 mitotic spreads could be counted from the testis of this animal, of which 4 had 27 chromosomes (the same as other *cristatellus)* and 6 had 28, or one extra chromosome. The extra chromosome appears to be a microchromosome. Possibly, the animal is a 27/28 mosaic. However, interpretation is difficult. Because of the small size of the microchromosomes, it is easy to have one masked by a large arm, and it is indeed possible that the real diploid number is 28. Ten counts are far too few to establish the karyotype with certainty. It should be emphasized that the two chromosomally aberrant *wileyae* did not differ morphologically from the other lizards sampled.

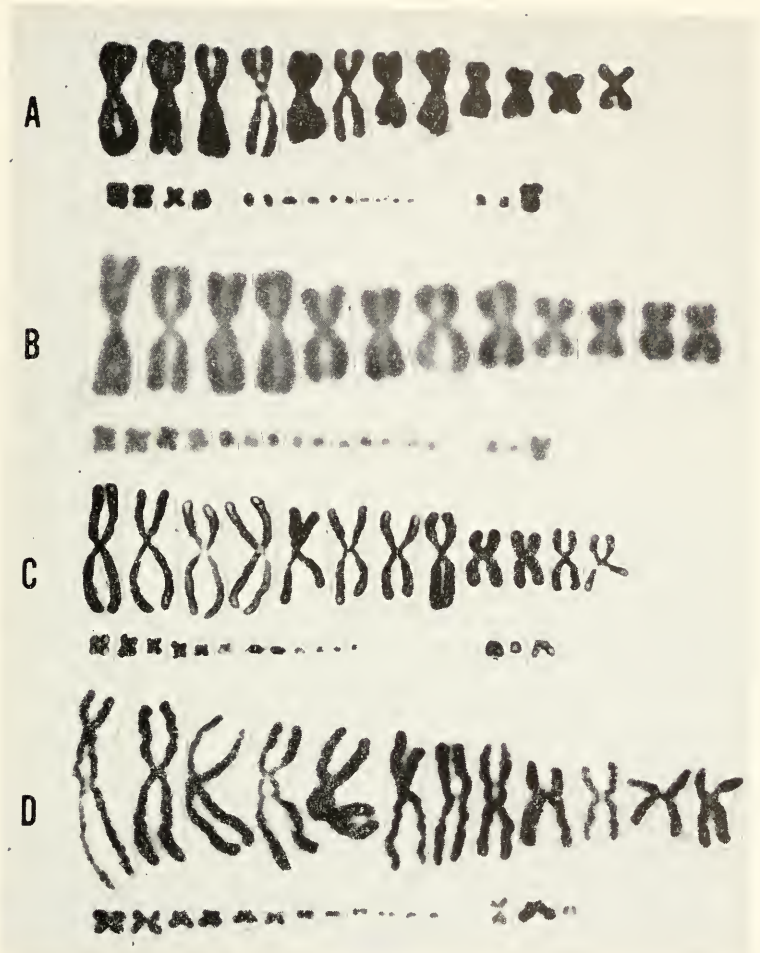

Figure 7. Mitosis in males of *cristatellus* group anoles. Giemsa stain.

A. *Anolis pulchellus* (2n=29). There are six pairs of metacentric macrochromosomes (top row), two pairs of small metacentric chromosomes (far left of second row), a sharp break between these and the five pairs of microchromosomes, and three unpaired sex chromosomes.

B. *A. cooki* (2n=29). Macrochromosomes as above (top row). Pairs seven and eight, small metacentrics, are as in *pulchellus*, but there is no sharp break between pair eight and pair nine. There are again three unpaired sex chromosomes.

C. *A. cristatellus wileyae* (2n=27). Macrochromosomes as in the above species. Microchromosomes most similar to *cooki*, but one pair fewer. Sex chromosomes similar.

D. *A. scriptus leucophaeus* (2n=27). Resembles *cristatellus*.

DISCUSSION

The chromosomal data support the hypothesis that *cooki* is a species distinct from *cristatellus*. This is in accord with observations made by Thomas in the field. There are two alternative explanations which may account for the observed chromosomal complements of these two species and their present-day distribution:

1. *A. cristatellus* has the lowest diploid number in its species group. Reduction in chromosome number is *usually* the derived condition and, if this be so in this case, *cristatellus* is a derived form. Chromosomal heterozygotes experience meiotic difficulties, leading to reduced fitness; the resultant structural mutants would be swamped in large populations. Chromosome structural changes, therefore, are probably established in small isolated populations. Thus it is logical to assume that the stock leading to *cristatellus* evolved in the limited population of a small island off Puerto Rico. Once chromosome loss had been established, *cristatellus* reinvaded the main island, successfully filling the lowland arboreal niche throughout Puerto Rico.

A. cooki has a very restricted range (southwestern Puerto Rico) and is specialized for a very dry rocky area. One hypothesis accounting for its origin is that it may have been isolated from its ancestral stock on an insular region corresponding to the present coastal hills of southwestern Puerto Rico. This stock, quite possibly the same one that gave rise to *cristatellus* (for the two species are remarkably similar in appearance), might have had the primitive karyotype for the species group.

The diploid number of *cooki* (29) is the same as that of *gundlachi* and the grass anoles of the *cristatellus* series, but there are some differences in the details of karyotype. The six pairs of macrochromosomes are comparable in all the forms. In *cooki* there is then a gradation from pairs 7 to 13, of which the largest three are metacentric (see Fig. 7), while in the grass anoles and *gundlachi* pairs 7 and 8 are medium-sized metacentrics which break sharply in size with the smaller pairs (9-13).

With respect to the microchromosomes, *cristatellus* resembles *cooki* in that pairs 7, 8, and 9 are all metacentric and grade in size into the smaller elements. The major difference, of course, is that *cristatellus* has one fewer pair of microchromosomes.

Hence we might postulate that *cooki,* although morphologically specialized, retains the primitive karyotype. *A. cristatellus,* then, is similar but has suffered chromosome loss, while *A. gundlachi* and the three grass anole species are the products of a single

radiation in which a new karyotype was established by reciprocal translocations from a species with the primitive (*cooki*-like) karyotype.

2. An alternative hypothesis would consider the *gundlachi*-type of karyotype primitive for the species group. *A. cristatellus* would again have been derived from a 2n=29 ancestor by chromosome loss, followed by minor rearrangements. The apparently closely related *A. cooki* might then have been directly derived from *cristatellus* by centric fission, which secondarily raised the male diploid number back to 29.

Karyotypic data, in any case, show that *gundlachi* is closer to the grass anoles than it is to *cristatellus*. This is not obvious from external morphology but is in accord with serum protein data (Maldonado and Ortiz, 1966) and osteological data (Etheridge, 1960). In karyotype, *gundlachi* is virtually indistinguishable from the grass anoles.

It is a further point of interest that the chromosomal evidence confirms the close relationship of *scriptus* and *cristatellus*. No other anoles of the 70 species and subspecies that we have studied have a male diploid number of 27, and even details of karyotype are identical.

From a glance at a map, one might expect that the southern Bahamas would be colonized from Hispaniola rather than Puerto Rico. However, as E. E. Williams pointed out to us, the general current flow is northwesterly, and there are several barely submerged banks between Puerto Rico and the southern Bahamas, banks which may have served as stepping stones for colonization. It is therefore not surprising to find a Puerto Rican derivative on these islands (see Fig. 4). The widespread Hispaniolan member of the *cristatellus* group, *A. cybotes*, has a diploid number of 36 in both males and females with no heteromorphism and could not possibly be the direct ancestor of *scriptus*.

The finding of apparent supernumerary chromosomes in two island populations of *A. c. wileyae* is of cytological interest, but lack of data at the present time on the extent of this variation within the populations and on the behavior of the supernumerary precludes discussion.

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BREVIORA

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DISTRIBUTION AND BIOLOGY OF THE OPISTHOPROCTID FISH *WINTERIA TELESCOPA* BRAUER 1901 [1]

Richard L. Haedrich and James E. Craddock[2]

INTRODUCTION

First taken by the German VALDIVIA Expedition in 1898, *Winteria telescopa* Brauer 1901 remained a unique oddity until Marshall (1960) reported a second specimen, Blache (1963) a third and fourth, and Bertelsen and Munk (1964) a fifth. Recent midwater trawl cruises, in particular those of the Woods Hole Oceanographic Institution in the Atlantic and of the ANTON BRUUN in the Indian and Eastern Pacific Oceans, have added significantly to this number. Twenty-three specimens are known, of which 18 have not been reported previously. This note records the specimens, compares them taxonomically, and offers some observations on the distribution and natural history of *Winteria*.

ACKNOWLEDGMENTS

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[1] Contribution No. 2031 from the Woods Hole Oceanographic Institution, and Papers from the "Dana" Oceanographical Collections No. 66.

[2] Woods Hole Oceanographic Institution, Woods Hole, Mass., and Museum of Comparative Zoology, Harvard University.

Figure 1. A young *Winteria telescopa*, 25.5 mm in standard length, from the Eastern Pacific (MCZ — 33°31′S, 77°29′W).

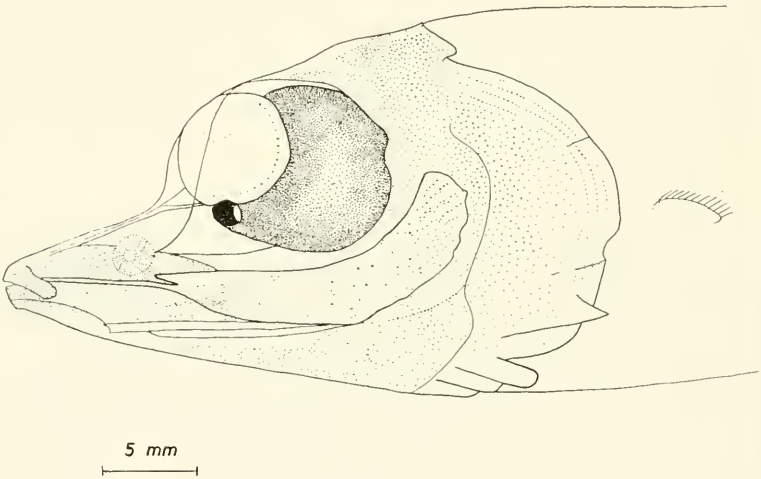

Figure 2. Head of an adult male *Winteria telescopa*, 91.5 mm in standard length, from the Eastern Pacific (USNM — 32°02′S, 73°48′W). Note the retinal diverticulum on the eye. The pinniform structure below the eye is a muscle, probably the adductor mandibulae, seen through the thin covering bone. Drawn by Martha M. Howbert.

and Robert H. Gibbs, Jr., United States National Museum, Washington, D. C. (USNM). Don Dockires, SIO, provided information on the sex of two Scripps specimens. The manuscript was read by Richard H. Backus and Giles W. Mead. Financial support has been provided in part by a United States Government Grant under the Fulbright-Hays Act to the senior author, and by the National Science Foundation through its support of the U. S. Program in Biology of the International Indian Ocean Expedition (IIOE) and the Southeastern Pacific Biological Oceanographic Program, and its grants GB-4424 (principal investigator Giles W. Mead) and GB-4431 (principal investigator Richard H. Backus) to the Woods Hole Oceanographic Institution.

MATERIAL EXAMINED

The following list of material, by ocean, indicates source institution (many specimens are as yet uncatalogued and hence have no catalog numbers), number of specimens, sex (if known), standard length in mm, and (in parentheses) vessel, cruise, station number or numbers, position, date, primary depths fished (no closing gear was used), and gear (IKMT = Isaacs-Kidd midwater trawl):

Atlantic — MCZ, 1 spec., ♀, 55 mm (CHAIN, Cruise 35, RHB-962, 5°24′N, 39°55′W, 13 Feb. 1963, 510-860 m, 10′ IKMT); MCZ, 1 spec., ♀, 83 mm (CHAIN, Cruise 35, RHB-976, 0°03′N, 27°31′W, 26 Feb. 1963, 565-675 m, 10′ IKMT); MCZ, 1 spec., ♀, 98.5 mm (ATLANTIS II, Cruise 20, RHB-1206, 11°01′N, 34°18′W, 23 Feb. 1966, 430-490 m, 10′ IKMT); TABL 14, 1 spec., 86 mm (GERONIMO, Cruise 2, sta. 82, 3°28′S, 01°14′W, 6 Aug. 1963); UMML 19998, 1 spec., 50 mm (PILLSBURY, sta. 295, 0°25′N, 5°09′E, 23 May 1965, 850 m, 10′ IKMT).

Indian — DANA, 1 spec., 100 mm (DANA, sta. 3847(3), 12°02′S, 96°43′E, 11 Oct. 1929, 2500 mwo, 300 cm Ring-trawl); MCZ, 1 spec., ♀, 115 mm (ANTON BRUUN, Cruise 3, Trawl 10 (AE-14), 2°06′S, 60°02′E, 21 Aug. 1963, 1600 m, 10′ IKMT); MCZ, 1 spec., ♂, 130 mm (ANTON BRUUN, Cruise 3, Trawl 11 (AE-15), 5°03′S, 63°10′E, 23 Aug. 1963, 685 m, 10′ IKMT).

Pacific — DANA, 1 spec., 82.5 mm (DANA, sta. 3716(3), 19°18.5′S, 120°13′E, 22 May 1929, 2000 mwo, 300 cm Ring-trawl); LACM, 1 spec., ♂, 124 mm (ELTANIN, Cruise 14, biol. sta. 1186, 52°10′S, 159°21′W, 4 Aug. 1964, 895-1030 m, 10′ IKMT); LACM, 1 spec., ♀, 147 mm (ELTANIN, Cruise 27, biol. sta. 1986, 45°33′S, 147°18′E, 26 Feb. 1967, 2840-3001 m, 5′

Blake Trawl); MCZ, 1 spec., 25.5 mm (ANTON BRUUN, Cruise 13, collection 40, 33°31′S, 77°29′W, 28 Jan. 1966, 425-820 m, 10′ IKMT); MCZ, 1 spec., 27 mm (ANTON BRUUN, Cruise 13, collection 43, 33°25′S, 77°38′W, 28-29 Jan. 1966, 100-380 m, 10′ IKMT); MCZ, 1 spec., 69 mm (ANTON BRUUN, Cruise 13, collection 58, 33°42′S, 72°17′W, 3 Feb. 1966, 400 m, 10′ IKMT); SIO, 1 spec., 33 mm (ANTON BRUUN, Cruise 12, SIO 65-664, 33°31′S, 75°18′W, 17-18 Dec. 1965, 530 m, 10′ IKMT); USNM, 1 spec., ♂, 91.5 mm (ANTON BRUUN, Cruise 14, sta. 550-A (RHG-66-9), 32°02′S, 73°48′W, 15 Feb. 1966, 200-500 m, 10′ IKMT).

Dr. Richard H. Rosenblatt has very kindly sent us counts and X-rays of three specimens in the collections at SIO. Pertinent data are: SIO 61-33, 1 spec., 70.5 mm (Monsoon Exped., sta. III-5, 10°39′S, 98°51′E, 22/23 Nov. 1960, 0-1500 m, 10′ IKMT. Counts: D 7, A 7, Pect. 12-12, Pelv. 8-8, vert. 34); SIO 61-37, 2 spec., 121.3 and 144.7 mm (Monsoon Exped., sta. IV-19, 33°19′S, 72°34′E, 19 Dec. 1960, 0-2000 m, 10′ IKMT. Counts: D 9 and 7, A 7 and 7, Pect. 12-13 and 12-13, Pelv. 9-9 and 8-9, Lat. line scales 35 and *ca.* 35, vert. 35 and 35, respectively).

DESCRIPTION

The following descriptive notes are provided to complement the characterizations of other opisthoproctids by Cohen (1964):

Body cylindrical, plump, becoming somewhat compressed at caudal peduncle, not particularly elongate. Belly lacking a sole. A rectal bulb and reflector organ present (Bertelsen and Munk, 1964). Eyes tubular and directed anteriorly. Interorbital very narrow. A dark-colored retinal diverticulum located anterolaterally on each eye. Snout elongate and hyaline; nasal capsules easily discerned. Branchiostegal rays 3, short and blunt. Gill membranes united across the isthmus. Maxillaries very small, thin and scale-like. Premaxillaries appear to be absent. No apparent teeth on the dentary. Swimbladder present (Marshall, 1960). Dorsal adipose fin present. Dorsal, anal, and ventral fins posteriorly placed; rays perhaps prolonged. Pectoral fins on peduncles, horizontally oriented high on the sides. Anus between pelvic fins, well before anal fin. Scales very deciduous.

Color in life deep blue-black with silvery overtones on the head. Fresh-caught specimens have a very plump body; preserved specimens are much shrunken in comparison.

TABLE 1

Proportional (Percent of Standard Length) and meristic data for *Winteria telescopa*.
Parentheses indicate a doubtful measurement due to damage. Holotype not examined; data derived from Brauer (1906).

	ANTON BRUUN-13 collection 40	ANTON BRUUN-13 collection 43	ANTON BRUUN-12 S10 65-664	PILLSBURY Sta. 295	CHAIN-3S RHB-962	ANTON BRUUN-13 collection 58	DANA 3716 iii	CHAIN-3S RHB-976	GERONIMO-2 Sta. 82	ANTON BRUUN-14 RHG-66-9	ATLANTIS II-20 RHB-1206	DANA 3847 iii	Holotype VALDIVIA Sta. 55	ANTON BRUUN-3 Trawl 10 (AE-14)	ELTANIN-14 Biol. Sta. 1186	ANTON BRUUN-3 Trawl 11 (AE-15)	ELTANIN-27 Biol. Sta. 1986	RANGE
Sex					imm. ♀			♀		♂	♀			♀	♂	♂	♀	♂ - ♀
Standard Length (mm)	25.5	27.0	33.0	50.0	55.0	69.0	82.5	83.0	86.2	91.5	98.5	100.4	112.5	115.0	124.0	130.0	147.0	25-147 mm
Head Length	39%	38%	36%	38%	36%	35%	33%	34%	34%	33%	33%	29%	32%	33%	31%	29%	32%	29-39%
Predorsal Oistance	70	72	68	67	68	68	68	66	67	69	66	66	65	70	67	65	70	65-72
Preanal Oistance	75	79	77	80	80	77	77	81	81	79	78	77	77	77	79	76	82	75-82
Prepelvic Oistance	63	63	64	64	64	62	62	64	64	63	65	65	61	64	65	62	69	61-69
Preanus Oistance	64	65	67	65	65	64	64	65	65	65	64	72	62	63	65	61	69	62-72
Maximum Oepth	22	21	22	22	22	20	19	22	20	20	22	18	20	22	20	20	23	18-23
Caudal Peduncle Oepth	11	9	9	11	10	10	10	10	10	10	11	10	11	10	11	11	11	9-11
Maximum Breadth	12	12	13	12	11	12	14	14	11	13	16	11	12	11	13	10	17	10-17
Dorsal Base Length	6	7	6	7	6	6	5	6	6	6	6	8	6	6	6	7	5	5-8
Anal Base Length	6	7	6	6	6	5	5	6	6	6	6	9	6	6	6	6	5	5-9
Longest Dorsal Ray	---	---	21	19	---	---	13	---	(6)	(6)	(6)	(7)	15	---	17	---	16	?-21
Longest Anal Ray	---	---	12	9	---	---	5	---	(4)	5	(5)	(4)	9	---	8	---	7	?-12
Pelvic Fin Length	10	---	14	---	---	---	8	---	5	6	---	8	---	---	10	---	9	5-14
Pectoral Fin Length	22	28	26	24	---	18	11	---	8	19	---	12	17	---	18	---	17	?-28
Snout Length	14	---	13	---	---	10	10	11	---	10	---	11	10	12	---	---	---	10-14
Eye Length	12	---	10	---	---	12	11	11	---	10	---	---	12	11	---	---	---	10-12
Eye Height	9	---	7	---	---	9	7	8	---	9	---	---	9	10	---	---	---	7-10
Counts:																		
Vertebrae	---	---	---	---	35	36	35	34	---	36	33	36	---	35	36	35	36	33-36
Lateral Line Scales	36	---	35	36	---	(35)	34	---	---	35	---	---	34	---	37	---	38	34-38
Dorsal Fin Rays	8	8	8	8	8	8	8	9	8	9	8	9	8	8	9	9	8	8-9
Anal Fin Rays	8	8	9	8	8	8	7	8	8	8	7	7	8	8	8	8	9	7-9
Pectoral Fin Rays	14	12	14	13	13	12	12	12	12	14	13	13	12	13	13	14	12	12-14
Pelvic Fin Rays	8	8	7	8	10	10	9	10	9	7	8	10	9	8	9	10	9	7-10
Ocean	E.PAC.	E.PAC.	E.PAC.	ATL.	ATL.	E.PAC.	W.PAC.	ATL.	ATL.	E.PAC.	ATL.	IND.	ATL.	IND.	S.PAC.	IND.	S.PAC.	

COMPARISON OF SPECIMENS

Morphometric and meristic data for 17 specimens, including Brauer's holotype of *Winteria telescopa,* are presented in Table 1. The small range of variation in both proportions and counts is strong evidence that there is but one species represented, and thus all our material is referred to *Winteria telescopa* Brauer 1901. There is perhaps some geographical variation in the number of vertebrae. The range is 33-35 vertebrae in the Atlantic, 34-35 in the Indian, and 35-36 in the Pacific. No pattern of variation is evident in the numbers of fin rays.

Little allometry occurs between 25 and 147 mm SL (Table 1). The only regular change is in the length of the head, which becomes relatively shorter with growth. This may be also true in the fins, although the rays are extremely fragile and are usually damaged.

As has been observed in the young of other opisthoproctids (Cohen, 1964), young *Winteria* (Fig. 1) somewhat resemble *Rhynchohyalus,* the genus linking the two divergent lines of the Opisthoproctidae. Characters found also in *Rhynchohyalus* are the elongate snout, the tubular eyes, the retinal diverticula ("orbital light organs" of Cohen, 1964, see Bertelsen *et al.,* 1965), the raised horizontal placement of the pectoral fins, and the insertion of the pelvic fins above the anus. With growth, the profile of the head in *Winteria* changes. The head becomes somewhat deeper in respect to its length, and the angle between the snout and the interorbital region is more pronounced (Fig. 2). This is in contradistinction to Brauer (1906: pl. I), who shows a smooth arc from the tip of the snout to the occiput.

DISTRIBUTION

Four of the previously known specimens of *Winteria* are from the tropical Atlantic off Africa (Brauer, 1901, holotype; Marshall, 1960, 1 spec.; Blache, 1963, 2 spec.), and have been referred by their recorders to *Winteria telescopa.* The fifth specimen was incidentally reported from the eastern Indian Ocean by Bertelsen and Munk (1964). The concern of their paper was anatomical, and they made no judgement as to the specfic status of their specimen, referring to it simply as *Winteria.*

As shown above, all specimens so far known can be referred to *Winteria telescopa* Brauer 1901. The distribution of this species is circumglobal (Fig. 3). The shallowest possible depth-of-capture (ANTON BRUUN 13-43) was certainly greater than 200 meters;

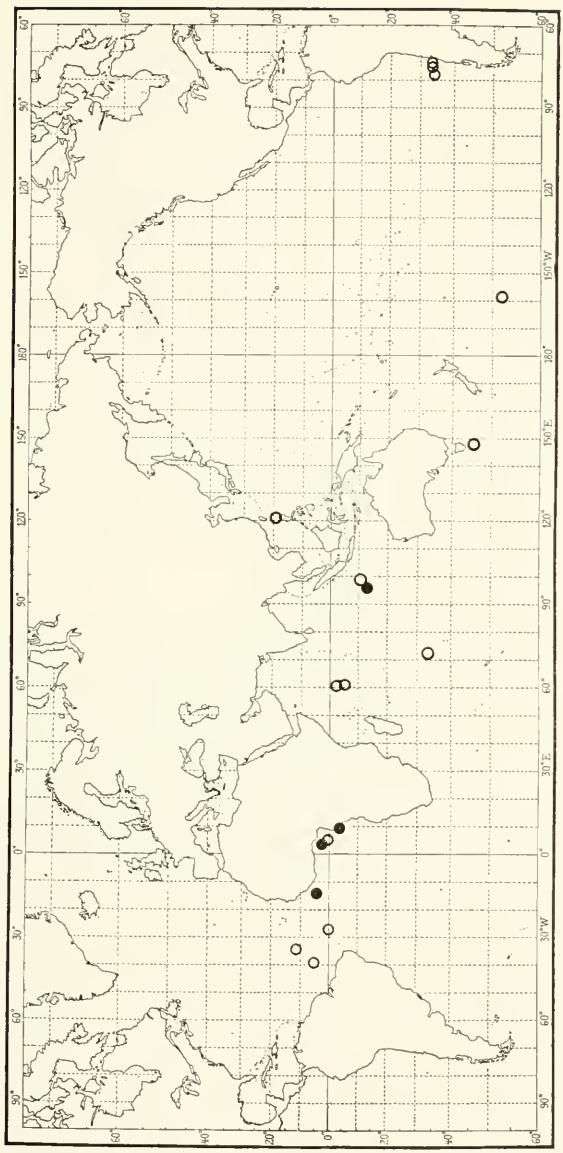

Figure 3. Positions of captures of *Winteria telescopa*. Closed circles indicate previously reported specimens; open circles are new records. Carlsberg Foundation base map.

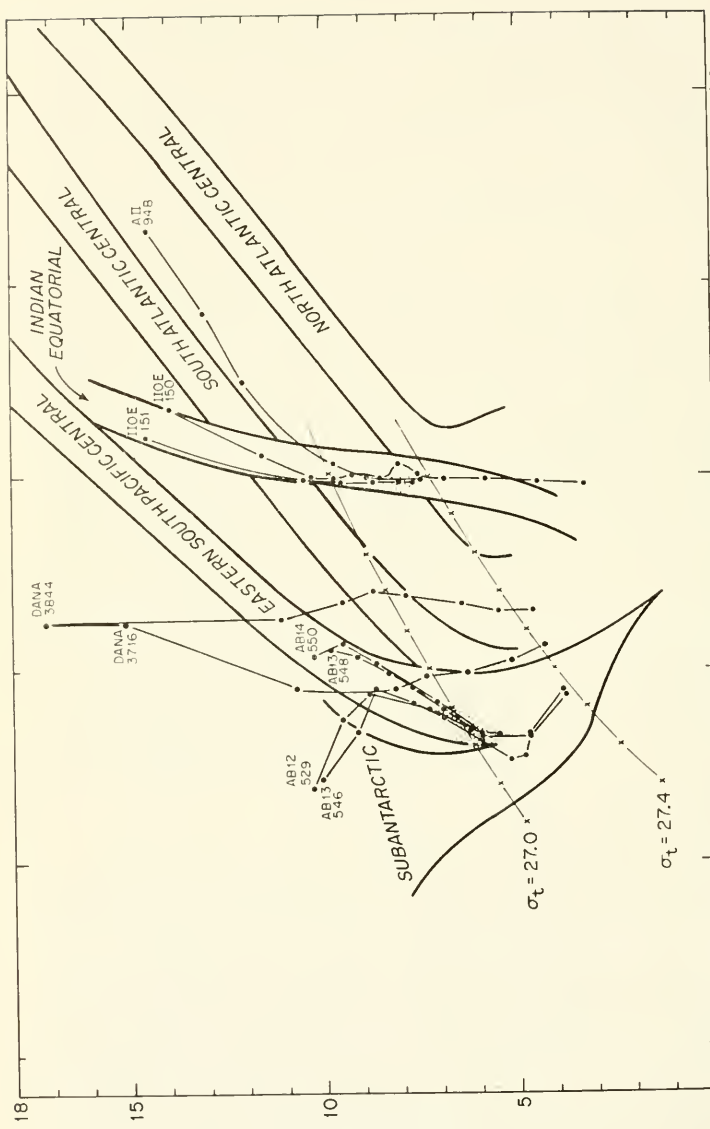

Figure 4. Temperature-salinity diagram with data plotted from those hydrographic stations adjacent to trawl stations capturing *Winteria*. Stippling indicates most probable depth-of-capture. See text. T-S envelopes from Sverdrup *et al.*, 1942.

the deepest tow (ELTANIN 1986) reached 3000 meters. The majority of captures probably occurred in the range 500-700 meters. *Winteria* then, like other opisthoproctids (Cohen, 1964), is a relatively deep-living fish.

Hydrographic casts had been made nearby or were made in connection with nine of the trawls which took *Winteria*. The temperature-salinity relationships at these stations, from 200 meters to the maximum possible depth-of-capture, are plotted in Figure 4. With the exception of the two western Indian Ocean stations (IIOE 150, 151), none falls entirely within a discrete water mass. They occur, for the most part, in the transitional regions between water masses, areas where the productivity is probably higher than in the generally poorer waters of the central gyres.

On the T-S curves of Figure 4, most probable depths-of-capture are indicated. When σ_t surfaces (density isopleths dependent upon temperature and salinity) are superimposed on the T-S plot, these depths fall within a σ_t range of 27.00 to 27.40. This suggests that the distribution of *Winteria* may be determined at least in part by density, a not unreasonable proposition. Pickford (1946) found that the distribution of *Vampyroteuthis,* a bathypelagic cephalopod, was restricted to the σ_t range 27.40 to 27.80.

REPRODUCTION

The gonads could not be distinguished in fishes smaller than 50 mm SL. Fishes between 50 and 90 mm appeared immature, with the onset of maturity occurring at about 90 mm SL. Both males and females could be recognized, and the gonads appear to be normal. There is no indication of hermaphroditism or viviparity. The ovaries of the three large females examined each contained two size classes of eggs, a 0.5-1.2 mm diameter group and a 1.8-2.5 mm diameter group (Table 2). These two size classes

Table 2. Standard length of female *Winteria* and numbers and sizes of eggs in one ovary.

Std. length	98 mm	115 mm	147 mm
N° small eggs	80	101	125
N° large eggs	59	102	171
Size range small eggs	.8-1.1 mm	.9-1.2 mm	.5-1.0 mm
Size range large eggs	1.8-2.2 mm	2.2-2.5 mm	2.0-2.5 mm

are present in about equal numbers. The data suggest a direct relationship between size of the fish and the number of eggs.

With the exception of the two Scripps specimens (SIO 61-37), all the *Winteria* were taken as single captures. The larger of the two fish which were taken together is a female containing large orange eggs; the smaller specimen appears to be a ripe or near-ripe male. *Winteria* is probably a solitary fish, encountering another of its kind only occasionally and pairing when ready to spawn.

FEEDING

The stomachs of the six largest specimens were opened. One was empty; the rest contained a finely divided, light yellowish, pulpy material. No structure could be discerned in this material, and we assume it was not composed of crustacean remains. It most closely resembled the finely shredded tissues of siphonophores, medusae, and salps found by Haedrich (unpublished) in the stomachs of stromateoid fishes.

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BREVIORA

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CAMBRIDGE, MASS. 29 MAY, 1968 NUMBER 295

THE CHAÑARES (ARGENTINA) TRIASSIC REPTILE FAUNA

IV. THE DICYNODONT FAUNA

C. Barry Cox[1]

The dicynodonts described in this paper were collected by the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology to the Permo-Triassic of western Argentina (Romer, 1966). Nearly all come from the Chañares Formation, the lithology and stratigraphic relationships of which have been described by Romer and Jensen (1966). They state (p. 12) that, "With one exception, all of the numerous vertebrate fossils found in the Chañares were from the lowest 10 meters or so of the formation." Eighteen dicynodont specimens were found in this fossiliferous band. One of these belongs to a new genus and species of dicynodont, described here as *Chanaria platyceps*. Eight specimens belong to a new species closely allied to *Dinodontosaurus turpior* from the Santa Maria Formation of Brazil (Cox, 1965); it is here named *Dinodontosaurus brevirostris*. Another specimen belongs to a second new species of this genus, here named *D. platygnathus*. Finally, an isolated large scapulocoracoid and clavicle show the presence of another genus of dicynodont. The remaining seven specimens are incomplete or badly damaged and therefore cannot be assigned with certainty to any of the named taxa.

In the accompanying figures, oblique shading indicates broken bone surface, horizontal shading indicates the presence of matrix, and broken lines indicate restored outlines of bone. The following abbreviations are used: MCZ — the Museum of Comparative Zoology, Harvard University; BYU — the Earth Sciences Museum, Brigham Young University, Provo, Utah; DGM — Divisão de Geologia e Mineralogia, Ministerio das Minas e Energia, Rio de Janeiro.

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Chanaria gen. nov.

Type species: *C. platyceps* sp. nov.

Diagnosis. Dicynodont of moderate size: skull length 33 cm. Teeth absent except for upper tusks. Greatest width of skull is across occipital region. Blunt anterior end to snout. Tusk projects anteroventrally. Lacrimal extends forwards on face, probably meets septomaxilla. No bony bosses on snout or on pineal region. Interorbital bar fairly wide. Frontal extends anteriorly into nasal as rectangular midline projection. Quite large prefrontal. Preparietal present, forming anterior border of pineal foramen. Postorbital bone extends well behind pineal foramen. Intertemporal bar narrow but concave in cross-section, not ridged. Squamosal does not extend on to intertemporal bar, posterior end of which is formed by interparietal. Short, wide temporal opening. Low, wide occiput; supraoccipital does not extend high up in midline.

Chanaria platyceps sp. nov.

Holotype. No. 65-XI-14-3 Museo de la Plata, La Plata, Argentina, skull. Collected by the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology.

Horizon and locality. From an exposure in the Triassic Chañares Formation about 6 miles east of the point where the Chañares River emerges into the Campo de Talampaya, in western La Rioja Province, Argentina.

Description. The type skull is 33 cm long and 30 cm wide. The mid-region of the palate, both quadrate regions, and part of the left side of the skull are missing.

Dorsal view (Fig. 1). The premaxilla extends a considerable distance posteriorly in the midline. There is only a short midline nasal suture, for the posterior regions of the nasals are separated by a rectangular anterior projection of the frontals. There is quite a large prefrontal; the posterior end of its suture with the frontal is uncertain, owing to damage. The interorbital bar is of moderate breadth.

The postorbital bone extends back to a point halfway between the pineal foramen and the posterior end of the intertemporal bar. The intertemporal bar is quite narrow, but it is slightly concave from side to side, without any midline ridge. The extreme posterior end of the bar is formed by the interparietal.

The occipital wing of the squamosal extends laterally, not posterolaterally. As a result, the posterior edge of the skull is almost straight and runs transversely, and the temporal opening is almost quadrilateral, its width approximately equalling its length.

Occipital view (Fig. 2). The occiput is rather low, its midline region being little higher than its more lateral parts. Most of the midline surface above the foramen magnum is formed by the interparietal rather than by the supraoccipital. The bones of the central occipital plate are fused together. The quadrate region and outer edge of the lateral wing of the squamosal are missing, but the dotted outline shown is the minimum extent of squamosal necessary to accommodate a quadrate of normal size.

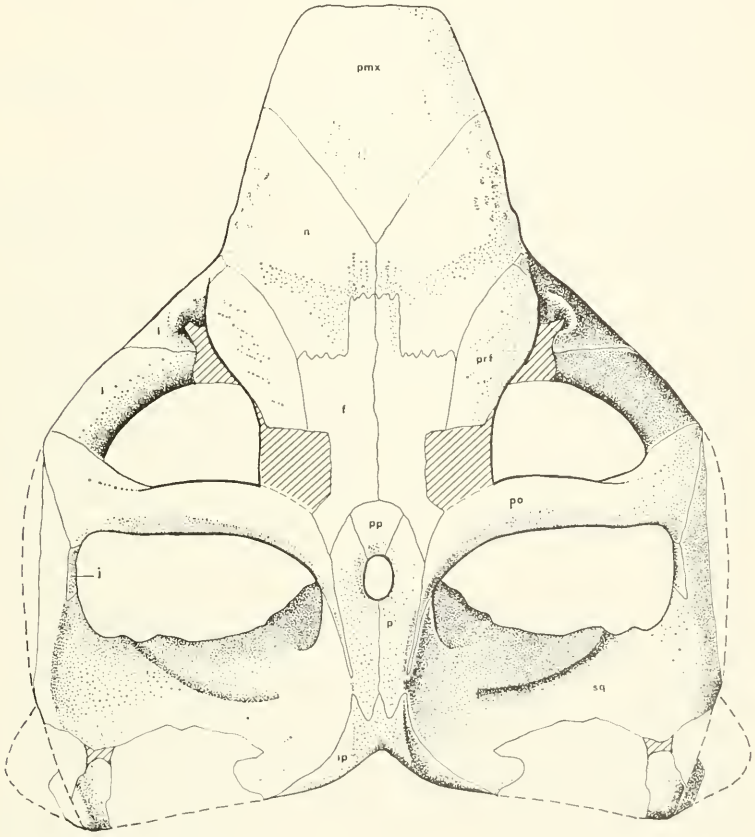

Figure 1. *Chanaria platyceps,* type specimen. Dorsal view of skull, x ⅓ (for abbreviations, see p. 26).

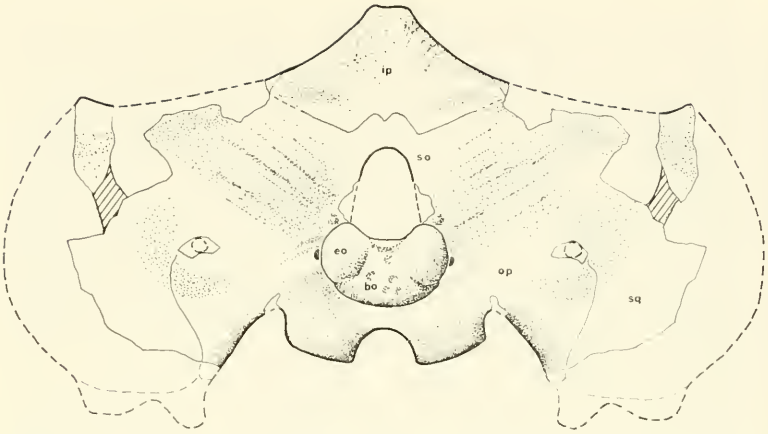

Figure 2. *Chanaria platyceps,* type specimen. Occipital view of skull. x ⅓ (for abbreviations, see p. 26).

Lateral view (Fig. 3). The powerful tusks project anteroventrally. The squamosal runs forward to meet the maxilla under the front half of the orbit.

A groove runs anteroventrally from the anterior corner of the nostril to the edge of the snout. A ridge which forms the lower edge of this groove also extends posteriorly along the maxilla behind the nostril. Above this ridge both the maxilla and the lacrimal curve slightly inwards, so that there is no sharply defined posterior border to the nostril. The lacrimal extends a considerable distance anteriorly and, though its anterior end and most of the septomaxilla are missing, it seems very probable that these two bones met, separating the nasal from the maxilla.

The palatal surface of the premaxilla bears the pair of anterior ridges and the median posterior ridge that are normal in the dicynodonts. The remainder of the ventral region of the skull is too incomplete to show any features of value.

Taxonomic position. In an earlier paper (Cox, 1965) I suggested that two main families of Triassic dicynodonts could be distinguished on the basis of the shape of the snout, the presence or absence of a median crest along the intertemporal bar, and the proportions of the occiput and of the temporal opening. In *Chanaria* the snout is wide and blunt, there is no median crest along

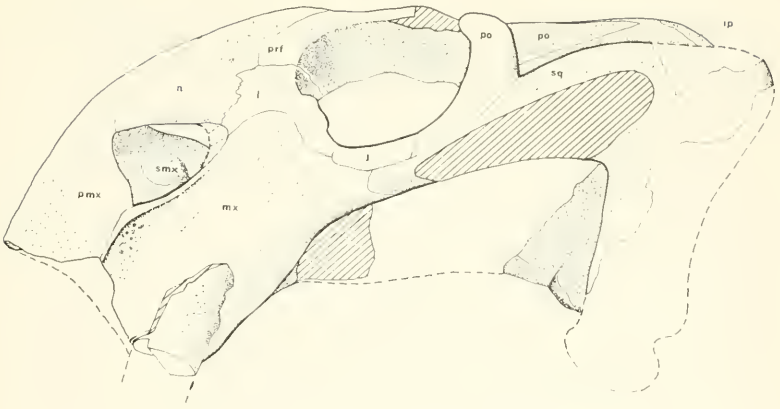

Figure 3. *Chanaria platyceps*, type specimen. Lateral view of skull, x ⅓ (for abbreviations, see p. 26).

the intertemporal bar, the occiput is wide but low, and the temporal opening is short. In all these characteristics, *Chanaria* clearly belongs to the family Stahleckeriidae.

Bonaparte (1966a) has since disagreed with my proposed classification of the Triassic dicynodonts into separate families. He believes that these forms are very uniform in structure, and that they are monophyletic in origin. Though I do not agree with either of these beliefs, Bonaparte's views and my own are, in the absence of knowledge of the Permian ancestry of the Triassic forms, subjective views of equal validity. The truth will emerge only from further work on the dicynodonts of the late Permian and early Triassic, and further discussion on these alternative classifications may be postponed until relevant material has been found and studied.

Dinodontosaurus brevirostris sp. nov.

Holotype. No. 65-XI-14-4 Museo de la Plata, La Plata, Argentina, skull. Collected by the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology.

Horizon and locality. From an exposure in the Triassic Chañares Formation about 6 miles east of the point where the Chañares River emerges into the Campo de Talampaya, in western La Rioja Province, Argentina.

Referred specimens. Specimen Nos. 3452-3457, Museum of Comparative Zoology, Harvard; specimen No. MR-120, Earth Sciences Museum, Brigham Young University, Provo, Utah.

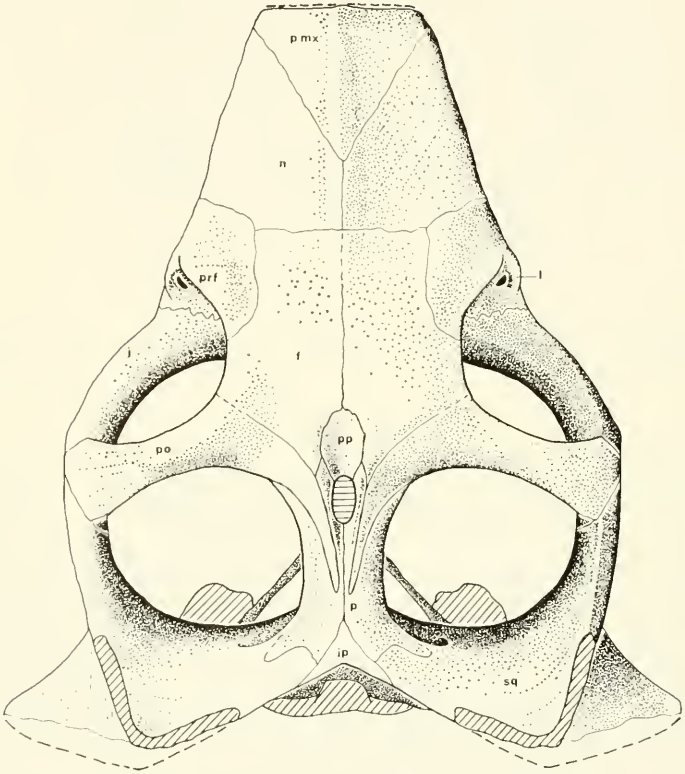

Figure 4. *Dinodontosaurus brevirostris,* type specimen. Dorsal view of skull, x ⅓ (for abbreviations, see p. 26).

Description. The skull of the type specimen, and those of specimens MCZ Nos. 3453 and 3457 and of specimen BYU No. MR-120, are all about 30 cm long. Specimen MCZ No. 3454 is 23 cm long and appears to be a juvenile. Other dicynodont remains from the Chañares Formation which cannot be certainly identified but which probably belong to this, the commonest dicynodont in the fauna, show that specimens nearly twice as large as the type were present.

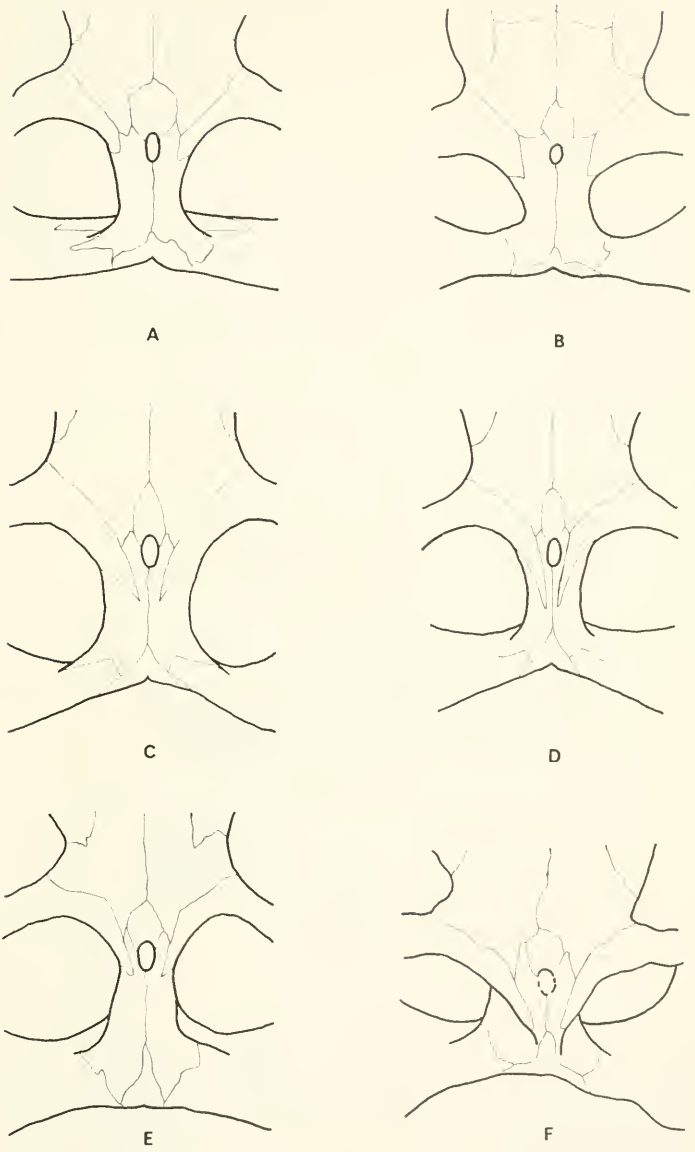

Figure 5. Dorsal views of pineal areas of specimens of *Dinodontosaurus*, reduced to equal size. A, *D. turpior,* MCZ No. 1628; B, *D. turpior,* MCZ No. 1687; C, *D. brevirostris,* MCZ No. 3454; D, *D. brevirostris,* type specimen; E, *D. turpior,* DGM No. 530R; F, *D. turpior,* DGM No. 213R.

Dorsal view (Fig. 4). *D. brevirostris* has the short temporal region and narrow, ridged intertemporal bar which are characteristic of the genus. However, there are some differences between *D. brevirostris* and the type species, *D. turpior,* in the relationships of the postorbital to the pineal opening. The postorbital of *D. brevirostris* approaches quite closely to the side of the pineal opening, and also extends posteriorly well beyond it. Though there is considerable range of variation in these characteristics in *D. turpior* (Fig. 5), the postorbital in that species is not normally as extensive as that of *D. brevirostris.*

Ventral view. The palate of the type specimen of *D. brevirostris* is too poorly preserved to show anything of value, but this area is well shown in the smaller specimen, MCZ No. 3454 (Fig. 6). The secondary palate extends posteriorly to a point level with the root of the canine tusks. The vomer and palatines do not form a bony

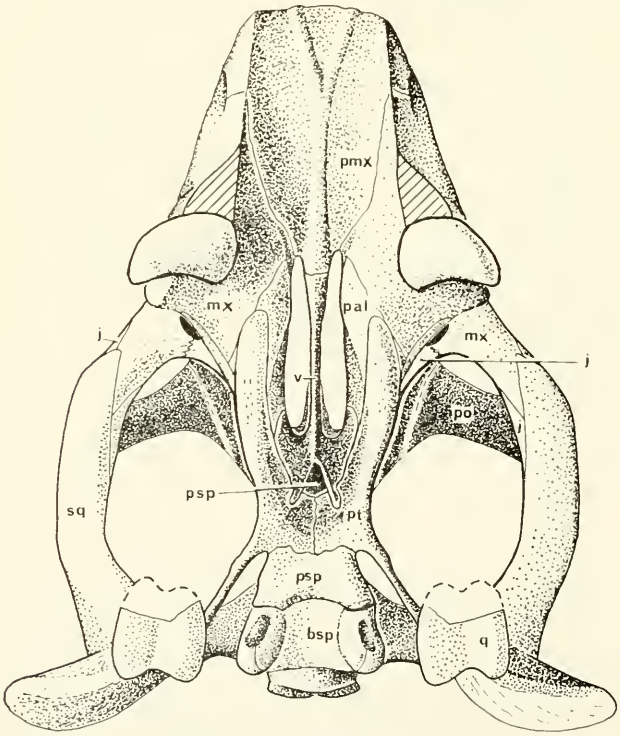

Figure 6. *Dinodontosaurus brevirostris,* MCZ No. 3454. Ventral view, x 4/9 (for abbreviations, see p. 26).

roof to the anterior part of the primary palate, between the anterior rami of the pterygoids. On either side of the median blade of the vomer there is therefore a clear passage dorsally (in the bony skull) to the ventral side of the bones of the skull roof (see also Fig. 9B). Behind the vomer, only a relic of the interpterygoid vacuity remains; through it is visible the ventral surface of the processus cultriformis of the parasphenoid.

The only specimen of *D. turpior* in which the median region of the palate is well preserved is specimen DGM No. 530R. In this[1] the vomer and palatines form a bony roof over a greater extent of the posterior part of the primary palate, and the median fusion of the pterygoids has extended further forward within the interpterygoid vacuity, so that the processus cultriformis is not visible from

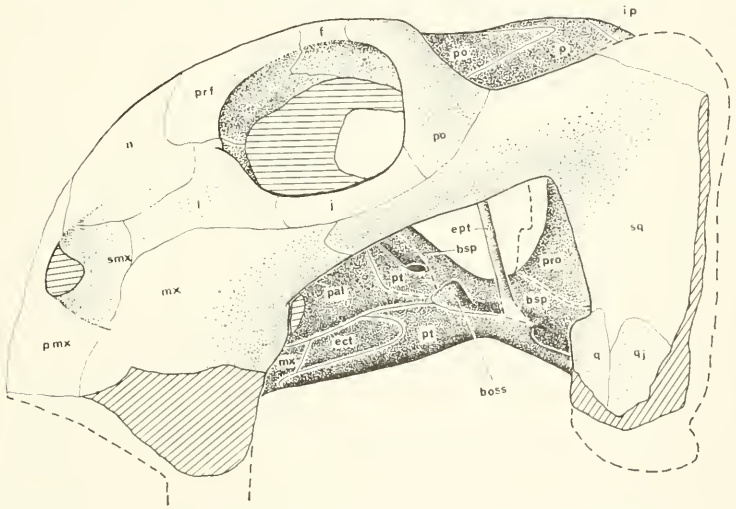

Figure 7. *Dinodontosaurus brevirostris,* type specimen. Lateral view, x ⅓ (for abbreviations, see p. 26).

[1]This specimen is of particular interest because it was described in 1936 by Tupí Caldas under the name *Diodontosaurus pedroanum,* a name which predates Romer's description of *Dinodontosaurus* (1943). However, Tupí Caldas's description is unfortunately so brief and so poorly illustrated that it cannot be regarded as a satisfactory basis for the identification of a new taxon, and *Diodontosaurus pedroanum* must therefore be regarded as a *nomen nudum.* The specimen has recently been more fully figured by Beltrão (1966).

below. However, it would be unjustifiable to assume that the two species differ in these features, as the smaller extent of these bones in specimen MCZ No. 3454 could merely be a result of its relative immaturity.

Side view (Fig. 7). The external naris is rather damaged but appears to be shallow, and there are no large foramina in the region of the septomaxilla. Though the edge of the maxilla where it forms the margin of the mouth is somewhat damaged, it is thin and was probably sharp-edged. This edge descends ventroposteriorly so that it reaches a considerable distance down the anterior border of the tusk.

Comparison of *D. brevirostris* with the specimens of *D. turpior* in the Museum of Comparative Zoology suggested that the snout of the Argentinian species was very much shorter, and the tusk much more ventrally directed, than in the Brazilian species. However, I was fortunately able to visit Rio de Janeiro and study the excellent material of *D. turpior* in the Divisão de Geologia e Mineralogia, Ministerio das Minas e Energia. This material has been prepared under the direction of Mr. L. I. Price, who has also made extensive studies of it. Examination of this material soon showed that the skull of specimen MCZ No. 1670 is very unusual in its long, low shape, and that there is a considerable range of variation in this region in *D. turpior* (Fig. 8). Nevertheless, there do appear to be two constant differences between the snouts of the two species. Firstly, the external naris of *D. brevirostris* is much closer to the anterior edge of the premaxilla than is that of *D. turpior*. Secondly, the tusk of *D. brevirostris* always projects directly ventrally, so that there is an abrupt angle between the body of the maxilla and the anterior end of the zygomatic arch, whereas there is a smoother transition between these regions in *D. turpior*. It is worth noting also that the lacrimal extends further forward on the face and meets the septomaxilla in all specimens of *D. brevirostris* in which the sutures of these regions are visible. This condition is known in *D. turpior* (Fig. 8F), but in that species these two bones are often separated by the maxilla.

There is a prominent boss on the dorsal surface of the palate, anterior to the base of the epipterygoid. This boss lies above a very distinct curving suture which separates it from the pterygoid, and it is therefore formed by the basisphenoid. Restudy of this area in *D. turpior* shows an identical situation, despite my statement that the boss in that species "is clearly part of the pterygoid" (Cox, 1965:482). Camp and Welles (1956:fig. 49) also show this boss as part of the basisphenoid in *Daptocephalus leoniceps*.

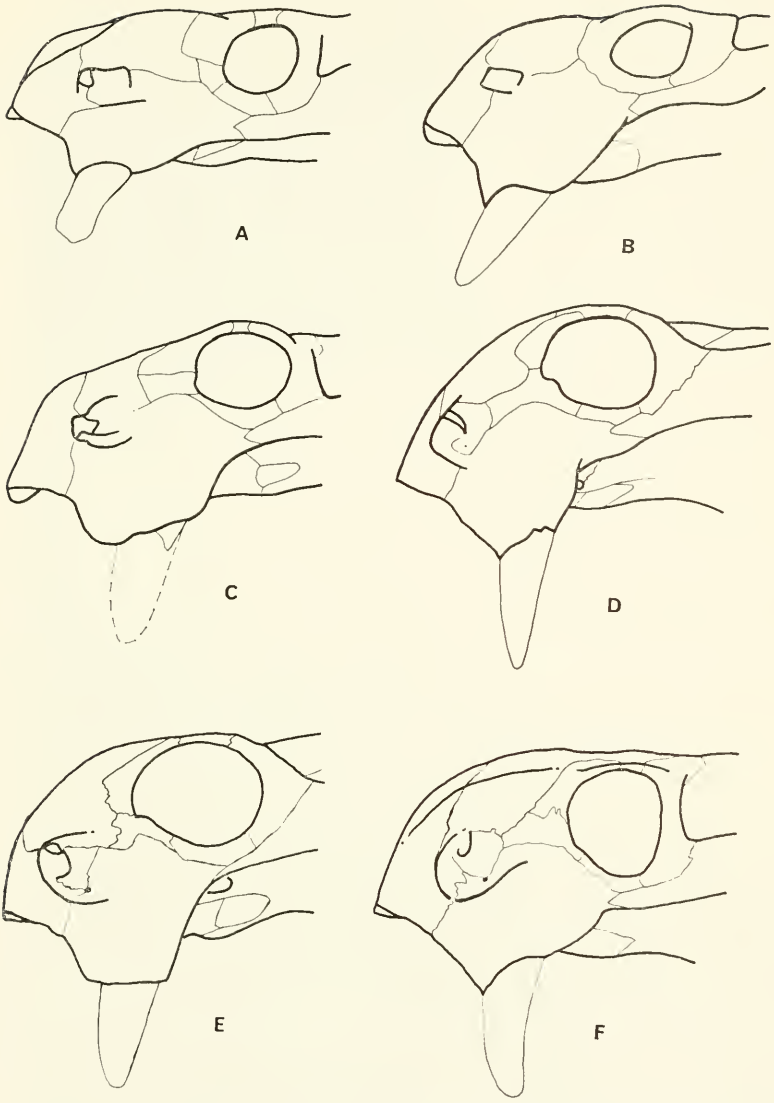

Figure 8. Lateral views of snouts of specimens of *Dinodontosaurus,* reduced to equal size. A, *D. turpior,* MCZ No. 1670; B, *D. turpior,* MCZ No. 1687; C, *D. turpior,* MCZ No. 1628; D, *D. brevirostris,* MCZ No. 3454; E, *D. turpior,* DGM No. 530R; F, *D. turpior,* DGM No. 309.

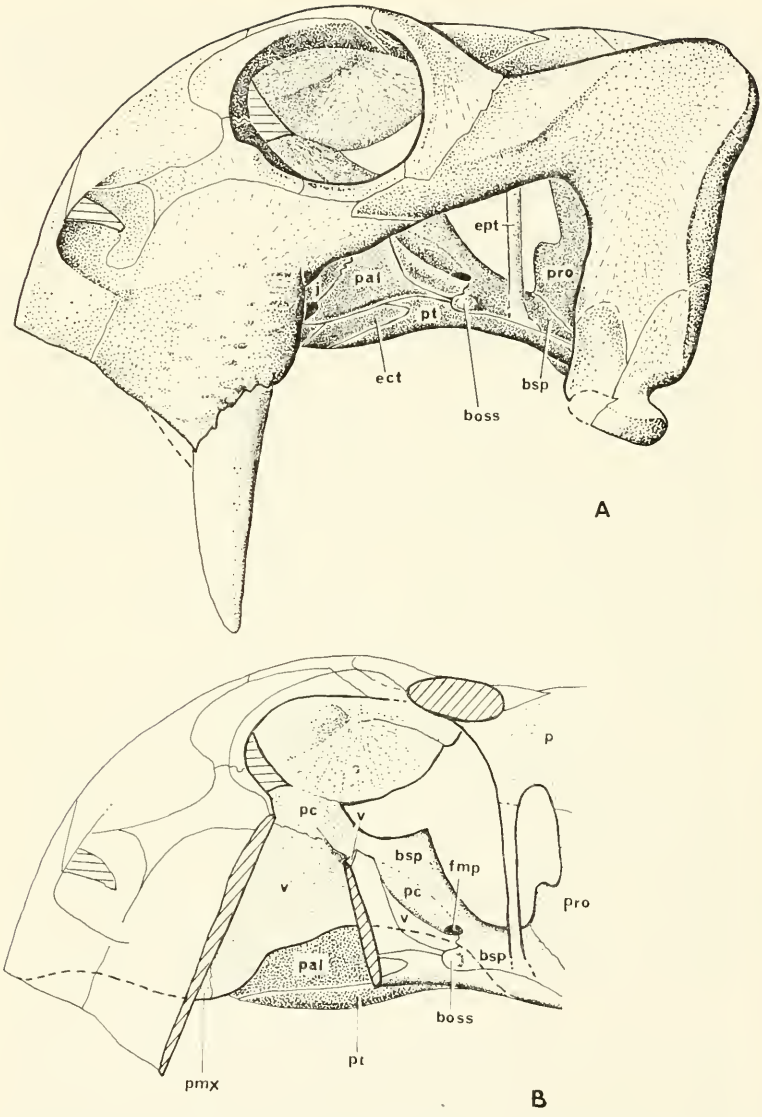

Figure 9. *Dinodontosaurus brevirostris,* MCZ No. 3454. Lateral views, x 4/9, A, of complete skull; B, after removal of suborbital bar, postorbital bar, anterior end of left half of palate, and part of left maxilla. Dotted lines in figure B show ventral outlines of midline regions of premaxilla, vomer and pterygoid (for abbreviations, see p. 26).

Further information on the structure of the dorsal roof of the palate and of the median interorbital-internasal septum is provided by specimen MCZ No. 3454 (Fig. 9A, B). This shows clearly that the ectopterygoid is present, confirming my earlier tentative identification of this bone in *D. turpior* (Cox, 1965). The palatine has an extensive exposure on the dorsal surface of the palate. It forms the lower border of the large foramen which runs forwards into the dental cavity of the maxilla; it extends dorsally to contact the parasphenoid, and runs back to meet the basisphenoid. Much of the palatine overlies the lateral wing of the vomer, which is visible in front of the palatine and also above its posterior extension, where the vomer forms the lower border of the dorsal end of the canal which runs forwards and upwards from the interpterygoid vacuity. As Klaauw and Roon (1942) have pointed out, this opening is not the simple equivalent of the old interpterygoid vacuity, and they have suggested that it be called the fenestra medio-palatinalis. The canal was probably traversed by a blood vessel. Since no such blood vessel is known in either *Sphenodon* (O'Donoghue, 1920) or *Ctenosaura* (Oelrich, 1956), it is impossible to identify it, though it seems most likely to have been a branch of the palatine artery.

Above the fenestra medio-palatinalis lies the medial region of the parasphenoid-basisphenoid complex. The processus cultriformis of the parasphenoid, as is normal in synapsids, continues anteriorly beyond the basisphenoid, and receives the lower edge of the sphenethmoid. The processus cultriformis is underlain by the vomer. This medial part of the vomer forms the lower part of the interorbital septum and also the posterior part of the internasal septum. It extends ventrally to meet the posterior end of the median palatal ridge of the premaxilla and has a total depth of 5.5 cm. The more dorsal portion of the interorbital septum is formed by the sphenethmoid (Fig. 9B).

More posteriorly, much of the rod-like epipterygoid is preserved in the young specimen, but its lower edge is damaged and the position of its suture with the parietal dorsally is uncertain. There are clear sutures between the prootic and the parietal, and between the prootic and the parasphenoid-basisphenoid complex.

All the specimens of *D. brevirostris* are tusked. Most of the tusks are broken off short, but the whole of the right tusk of specimen MCZ No. 3453 is preserved and shows clear signs of wear. The outer surface of the distal end of the tusk is worn, so that its tip lies near its posteromedial edge. Traces of other wear facets

are also visible on the posteromedial surface of this specimen, but are better shown in an isolated tusk, specimen MCZ No. 3452 (Fig. 10A-C).

In longitudinal section of a tusk, the dentine appears to consist of a series of V-shaped bands; in a tusk about 15 cm long and 2.5 cm in diameter at its base, these bands are about 2.5 mm thick (Fig. 10E). They are caused by alternating light and dark zones of dentine, which are apparently due to slight variations in the concentration or thickness of the dentinal tubules. Further bands, which are similar but only a few tenths of a millimetre in diameter, are also visible in thin sections examined under a microscope.

A system of cracks, which in general parallel this system of V-shaped bands in the dentine, can also be seen in longitudinal section (Fig. 10D), and appear as concentric circles in transverse section of the tusk. A similar system has been described in *Placerias* and *Kannemeyeria* by Camp and Welles (1956). However, these cracks are not related to the above-mentioned variations in the structure of the dentine, and appear to be post-mortem. The cracks merely reflect the main plane of structural weakness in the dentine, which in turn is related to its mode of deposition.

The base of the tusk is open and it probably grew continuously. A series of annular grooves can also be seen around that portion of the tusk which lies within the maxilla; this has also been noted by Camp and Welles (1956). Similar annular grooves and variations in dentinal structure (alternating between columnar and marbled dentine) have been described in the elephant seal *Mirounga leonina* by Laws (1953). He has shown that the pattern of banding in that animal is complex, but that there is a regular annual repetition of this pattern. The details of the annual pattern also differ between the sexes, due to their different cycles of activity during the breeding season. It is unfortunately impossible to verify whether these features in *Dinodontosaurus* are similarly related to age or sex. This would be expected only if the climate were sufficiently seasonal to cause variations in the rate of growth of both sexes, or if variations resulted from such seasonal activities as egg-laying.

Postcranial material. Specimens MCZ Nos. 3454, 3455 and 3456 all included postcranial material; that belonging to specimen MCZ No. 3455 is particularly well preserved. However, none of this material shows significant differences from the corresponding bones of *D. turpior,* or adds to our knowledge of the postcranial skeleton of the genus.

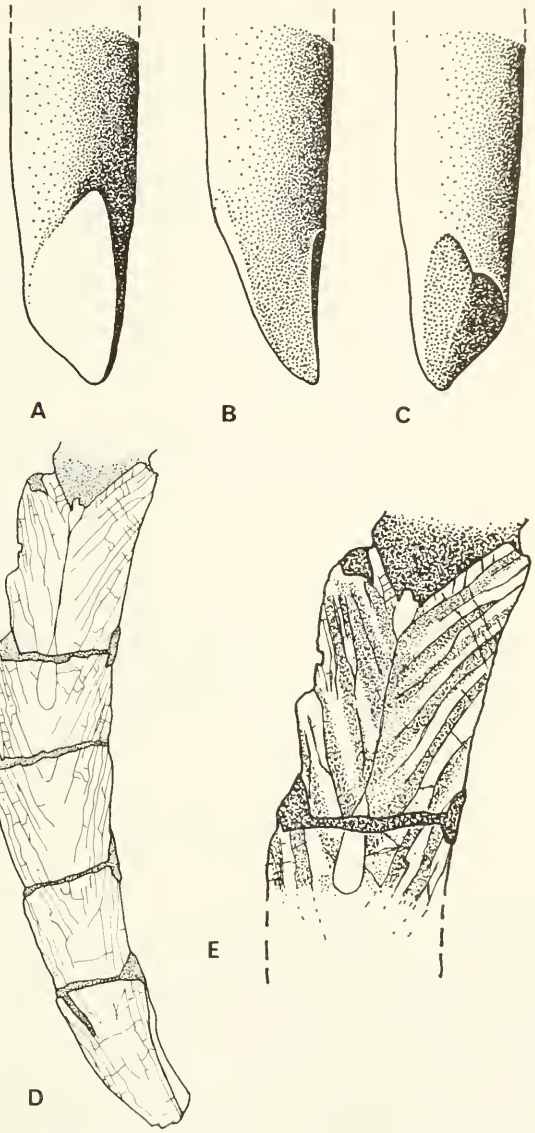

Figure 10. *Dinodontosaurus brevirostris.* A-C, right tusk of specimen MCZ No. 3452 showing wear facets, x ⅔. A, lateral view; B, anterior view; C, medial view. D, E, longitudinal sections of part of tusk of specimen MCZ No. 3456. D, showing system of cracks, x ⅔; E, showing pattern of bands in dentine, x 1.

DINODONTOSAURUS PLATYGNATHUS sp. nov.

Holotype. No. 65-XI-14-5 Museo de la Plata, La Plata, Argentina, fragmentary skull and lower jaw. Collected by the 1964-1965 expedition of the Museo de la Plata and the Museum of Comparative Zoology.

Horizon and locality. From an exposure in the Triassic Chañares Formation, about 1¼ miles north-north-west of the point where the Gualo River emerges from the Plano del Gualo, in western La Rioja Province, Argentina.

Referred material. Specimen No. 149R, Divisão de Geologia e Mineralogia, Ministerio das Minas e Energia, Rio de Janeiro.

Description. The type specimen consists only of the palatal and occipital regions of a large skull, and of an almost complete lower jaw (Fig. 11). The bluntly-ending snout and the presence of downwardly directed canine tusks show that the specimen probably belongs to the genus *Dinodontosaurus.* The anterior end of the lower jaw, however, is elongated and tapers to a relatively thin

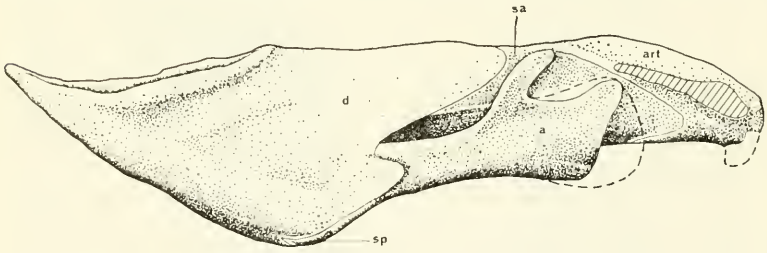

Figure 11. *Dinodontosaurus platygnathus,* type specimen. Lateral view of lower jaw, x ⅓ (for abbreviations, see p. 26).

point, unlike that of *Dinodontosaurus turpior.* It at first seemed likely that this was merely an aberrant type of distortion, but the existence of an almost identical lower jaw (specimen No. DGM 149R) in the Rio de Janeiro collection from the Santa Maria Formation of Brazil makes this explanation less plausible, and suggests instead that a different species of *Dinodontosaurus* may be represented. The fragments of the palate and occiput associated with the type specimen unfortunately do not show any other features by which the species could be distinguished from *D. turpior,* but it is felt nevertheless that the characters of the lower jaw merit specific distinction as *Dinodontosaurus platygnathus.*

KANNEMEYERIID REMAINS FROM THE CHAÑARES FORMATION

Specimen MCZ No. 3459 comprises a large left scapulocoracoid and clavicle; it was found about two miles east of the Mogote del Gualo (see Romer and Jensen, 1966, fig. 2).

The scapulocoracoid is badly flattened. As preserved, it has a total length of 63.5 cm, the scapula itself being about 48 cm long (Fig. 12). The scapula is very markedly constricted, being only 8 cm across at its narrowest point but expanding to 25 cm wide at its upper end. Most of the spine down the outer surface of the scapula has been eroded away but, from the width of its base and from the contours of the surrounding bone, the spine was clearly well developed and its dorsal end rose rapidly upwards from the blade. A groove runs down the inner surface of the lower end of the scapula. This groove leads to the coracoid foramen, which lies within the precoracoid bone.

The incomplete clavicle measures 33.5 cm along its outer surface, which is slightly convex longitudinally.

As discussed in an earlier paper (Cox, 1965), the shape of the scapula seems to be one of the diagnostic features of the two main families of Triassic dicynodonts. Short, wide scapulae are found in the Stahleckeriidae, which includes the other Chañares dicynodonts (*Chanaria* and *Dinodontosaurus*). Tall, narrow-waisted scapulae are, on the other hand, characteristic of the Kannemeyeriidae, which includes the genera *Kannemeyeria, Parakannemeyeria, Sinokannemeyeria, Barysoma* and *Ischigualastia.* The scapula of MCZ No. 3459 is very similar to that of *Barysoma,* which is known from some postcranial material and an occipital plate from the Santa Maria Formation of Brazil (Romer and Price, 1944; Cox, 1965). The scapula of MCZ No. 3459 and that of *Barysoma* resemble one another closely in shape and in the position and strength of the spine. The scapula of *Barysoma* is, however, considerably larger; though incomplete, it is 55.5 cm long.

The single scapulocoracoid and clavicle of MCZ No. 3459 do not, of course, provide sufficient evidence to claim that *Barysoma* was present in the Chañares Formation or, alternatively, to erect a new genus or species of dicynodont. The specimen is merely evidence that the kannemeyeriid dicynodonts existed in Argentina during the time that the Chañares Formation was deposited. This is not surprising, since kannemeyeriids are known in Argentina both from the earlier Puesto Viejo Formation (Bonaparte, 1966a) and from the later Ischigualasto Formation (Cox, 1965).

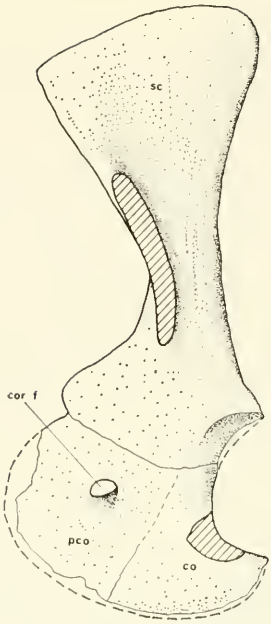

Figure 12. Scapulocoracoid of specimen MCZ No. 3459, x ⅛ (for abbreviations, see p. 26).

DICYNODONT REMAINS FROM THE TARJADOS FORMATION

A few fragmentary dicynodont remains were also collected in the transitional beds underlying the thick white sandstones which form the upper part of the Tarjados Formation. Specimen MCZ No. 3468 was collected just north of the Plano del Gualo, about one mile west of the Mogote del Gualo (see Romer and Jensen, 1966, fig. 2); it includes fragments of a skull and lower jaw. The maxilla encloses the proximal portion of a powerful tusk about 3.0 cm in diameter. This tusk shows traces of the alternating bands described above in *Dinodontosaurus brevirostris,* but also bears several longitudinal furrows. The remaining two specimens from the Tarjados Formation may also belong to the Dicynodontia: two fragments of large limb bones (MCZ No. 3469) and fragments of ribs (MCZ No. 3467).

THE AGE OF THE CHAÑARES FAUNA

The commonest Chañares dicynodont is *Dinodontosaurus brevirostris*. This species is extremely closely related to *Dinodontosaurus turpior*, which is the commonest dicynodont of the Santa Maria Formation of Brazil. The two species differ only in that the nostril of *D. brevirostris* is slightly closer to the front edge of the premaxilla, and its postorbital bone extends closer to, and further behind, the pineal foramen. This degree of similarity between their most abundant types of dicynodont is very strong evidence that the two faunas are very close in age. This is supported by the presence in both faunas of the peculiar elongated type of dicynodont jaw, which has here been named *Dinodontosaurus platygnathus*. The Chañares fauna, however, lacks *Stahleckeria*, a dicynodont which occurs with *Dinodontosaurus* in the Santa Maria fauna; this suggests that the two faunas are not identical in age. In the slightly greater extent of its postorbital, *D. brevirostris* is more primitive than *D. turpior*, and it may well be ancestral to the Brazilian species; this suggests that the Chañares fauna is slightly earlier than the Santa Maria fauna.

Another fauna which appears to be earlier than that of the Santa Maria Formation is that of the Manda Formation of East Africa (Cox, 1965). This includes the dicynodont genus *Kannemeyeria*, found also in the early Triassic Cynognathus Zone fauna of South Africa, and differs from the Santa Maria fauna in containing a more primitive type of rhynchosaur (Colbert, 1958) and in lacking dinosaurs. Since both the Manda fauna and the Chañares fauna thus appear to be earlier than the Santa Maria fauna, it is necessary next to discuss the relative ages of these two faunas.

As just noted, the strong similarity between the dicynodonts of the Chañares fauna and those of the Santa Maria fauna strongly suggests that these two faunas are very close in age. In view of the considerable differences between the Santa Maria fauna and the Manda fauna, this further implies that the Chañares fauna is probably later than the Manda fauna. However, Romer (1966) has, on the contrary, suggested that the Chañares fauna is the earlier of the two. The evidence provided by the other elements of these faunas (cynodonts, pseudosuchians and rhynchosaurs) must therefore be examined.

The traversodontid *Massetognathus* is the only Chañares cynodont so far described (Romer, 1967). Each of the upper cheek teeth of this genus "shoulders" slightly into the one ahead; their crowns each bear two external cusps and a cross-ridge which lies

at the extreme posterior edge of the tooth so that the crown consists of a single basin. The traversodontid of the Manda fauna is *Scalenodon,* in which the upper cheek teeth do not "shoulder" into one another, the crown of the tooth bears only a single external cusp, and the cross-ridge lies more anteriorly, so that it divides the crown into anterior and posterior basins. The upper cheek teeth of later Triassic traversodontids such as *Proexaeretodon* and *Exaeretodon* of the Ischigualasto Formation, on the other hand, are similar to those of *Massetognathus,* but the "shouldering" of one tooth into the next is more pronounced. As Romer (1967: 20) states, "These differences suggest that *Scalenodon* is rather more primitive than the described South American forms." Furthermore, trirachodontid cynodonts are present in both the Manda Formation and in the earlier Cynognathus Zone fauna of South Africa, but are absent in the Chañares fauna. The relationships among all these cynodont faunas are thus more easily explained if the Chañares fauna is later than that of the Manda.

Romer (1966) has stated that the Chañares fauna contains small thecodonts similar to *Euparkeria* of the Cynognathus Zone. Other, more advanced pseudosuchians are also present, however, and our knowledge of the Chañares pseudosuchians is as yet too incomplete to provide any basis for a dating of the fauna.

Rhynchosaurs are absent from the Chañares fauna, but are found in both the Manda fauna and the Santa Maria fauna. As noted by Romer (1967), this fact is more easily explained if the Chañares fauna is older than that of the Manda and represents a time at which the rhynchosaurs were not yet developed as a major faunal element. However, rhynchosaurs are also unknown in two of the three localities in the Santa Maria Formation, and the composition of the fauna of these two localities is exactly the same as that of the Chañares fauna: dicynodonts (mainly *Dinodontosaurus*), cynodonts and pseudosuchians. Rhynchosaurs are known in the Santa Maria Formation only from a third locality, in which dicynodonts are absent (von Huene, 1935-42; Bortoluzzi and Barberena, 1967). These facts suggest that, though rhynchosaurs and dicynodonts are found together in the earlier Manda fauna, the ecological preferences of the South American type of rhynchosaur were distinct from those of the dicynodonts of these faunas, so that these groups are rarely preserved together — and it is relevant to note here the extremely specialised dental apparatus of the rhynchosaurs. If this is true, it is neither surprising nor significant that rhynchosaurs have not been found in the Chañares fauna.

To summarize, none of the evidence from the other vertebrate groups provides a convincing reason for rejecting the conclusion (based on the dicynodonts) that the Chañares fauna is only slightly earlier than that of the Santa Maria Formation of Brazil; it further appears to be later than that of the Manda Formation of East Africa.

One may next attempt to assess the relative ages of these South American Triassic faunas. The Chañares Formation of Argentina is somewhat older than the Los Rastros Formation, by which it is conformably overlain. On the other hand, it is also, on the evidence of the species of *Dinodontosaurus,* somewhat older than the Santa Maria Formation of Brazil, which may therefore be regarded as equivalent in age to the Los Rastros Formation of Argentina. Unfortunately, vertebrate fossils have not been found in the Los Rastros Formation, so it is impossible to confirm the equivalence by direct faunal comparison. The footprints of *Rigalites* from the Los Rastros Formation could, however, well have been made by one of the large pseudosuchians of the Santa Maria Formation (Bonaparte, 1966b).

There is also no unconformity between the Los Rastros Formation and the Ischigualasto Formation in the Chañares area, but merely a decrease in the amount of sandstone and an increase in the amount of clay and shale. Despite this lack of any break between the two formations, and the similarity between their cynodonts and rhynchosaurs, the archosaurs of the Ischigualasto fauna are considerably more advanced than those of Los Rastros/Santa Maria age.

Finally, it is impossible to equate these Gondwanaland vertebrate faunas to the standard German and Alpine divisions of the Northern Hemisphere Triassic with any degree of accuracy (Romer, 1966; Cox, 1967). One can at present only attempt to define the extreme limits between which these faunas must lie. As argued earlier, even the Chañares fauna is younger than the Manda fauna of East Africa. The latter contains the pseudosuchian reptile *Mandasuchus,* which is very similar to the genus *Ticinosuchus,* found in a definitely Anisian level of Monte San Giorgio, Switzerland (Krebs, 1965; Charig, MS in preparation). All these South American faunas are therefore probably post-Anisian. At the other extreme, even the Ischigualasto fauna is earlier than the Upper Norian, since it contains armoured pseudosuchians but lacks coelurosaurs and large dinosaurs (cf. Chowdhury, 1965). In fact, this fauna is probably somewhat earlier than Norian: Bonaparte (1966b), after reviewing the whole Ischigualasto fauna, has concluded that it is probably of Carnian age.

These conclusions are similar to those of Stipanicic, which are based upon evidence from fossil floras and ammonites, and which may be briefly considered here. The palaeobotanical evidence consists of the presence in the Los Rastros Formation (among others) of a flora which contains both Gondwanic *Dicroidium* elements and also a considerable number of Northern Hemisphere species (Stipanicic, 1957). Stipanicic points out (In press) that the northern species are known in the Northern Hemisphere only in deposits of post-Ladinian age. However, the range of these species into the earlier Triassic is still unknown, and this evidence therefore cannot yet be regarded as conclusive.

The ammonite evidence consists of the presence of specimens, identified by Barthel (1958) as *Cuccoceras* n.sp.aff. *cuccense* and *Beyrichites* sp., in beds lying under the igneous Pastos Grandes Group in Chile. According to Stipanicic (1967), this group practically interfingers with the Choiyoilitense Group of Argentina. Stipanicic (In press) believes that the Choiyoilitense Group is part of an igneous complex which is to be found below the various fossil vertebrate faunas and below the *Dicroidium* flora. Since the ammonites mentioned above indicate an Upper Anisian age, the overlying igneous complex and the fossil faunas and floras must all be post-Anisian. However, Kummel (personal communication) feels that the ammonite specimens are too incomplete for a definite taxonomic identification, and this line of argument must therefore be regarded as unproved.

SUMMARY

Three new stahleckeriid dicynodonts from the Chañares Formation of Argentina are described: *Chanaria platyceps* gen.et sp.nov., *Dinodontosaurus brevirostris* sp.nov., and *Dinodontosaurus platygnathus* sp. nov. A few post-cranial remains suggest that a kannemeyeriid dicynodont was also present.

Dinodontosaurus brevirostris is very closely related to *Dinodontosaurus turpior* of the Santa Maria Formation of Brazil, and is probably directly ancestral to it. The Santa Maria Formation therefore appears to be only slightly younger than the Chañares Formation, and equivalent to the Los Rastros Formation of Argentina.

The Chañares fauna is therefore younger than the Manda fauna of East Africa; this conclusion is supported by the cynodonts of these faunas. Though rhynchosaurs are absent from the Chañares fauna, this is also true of two of the three localities in the Santa Maria Formation, and their absence is almost certainly merely ecological.

The Chañares, Santa Maria and Ischigualasto faunas are, collectively, probably of Ladinian to Carnian age.

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LIST OF ABBREVIATIONS USED IN THE FIGURES

a	angular
art	articular
bo	basioccipital
bsp	basisphenoid-parasphenoid complex
co	coracoid
cor f	coracoid foramen
d	dentary
ect	ectopterygoid
eo	exoccipital
ept	epipterygoid
f	frontal
fmp	fenestra medio-palatinalis
ip	interparietal
j	jugal
l	lacrimal
mx	maxilla
n	nasal
op	opisthotic
p	parietal
pal	palatine
pc	processus cultriformis
pco	precoracoid
pmx	premaxilla
po	postorbital
pp	preparietal
prf	prefrontal
pro	prootic
psp	parasphenoid

pt	pterygoid
q	quadrate
qj	quadratojugal
s	sphenethmoid
sa	surangular
sc	scapula
smx	septomaxilla
so	supraoccipital
sp	splenial
sq	squamosal
v	vomer

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